SHOUT
SHARE
IT

THE ANNALS OF APPLIED BIOLOGY

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, Manager
LONDON: FETTER LANE, E.C. 4

H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. I
WILLIAM WESLEY & SON, 28, ESSEX STREET, LONDON, W.C. 2
PARIS: LIBRAIRIE HACHETTE & CIE.
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TORONTO: THE MACMILLAN CO. OF CANADA, LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

All rights reserved

THE ANNALS OF APPLIED BIOLOGY

THE OFFICIAL ORGAN OF THE ASSOCIATION
OF ECONOMIC BIOLOGISTS

EDITED BY
E. E. GREEN, Way's End, Camberley (late Government Entomologist, Ceylon)
WITH THE ASSISTANCE OF THE COUNCIL

VOLUME VI 1919–20

CAMBRIDGE
AT THE UNIVERSITY PRESS
1920

CONTENTS

No. 1 (September, 1919)

PAGE

1. Physiological Pre-Determination: the Influence of the Physiological Condition of the Seed upon the Course of Subsequent Growth and upon the Yield. V. Review of Literature. Chapter IV. By FRANKLIN KIDD, M.A. (Cantab.), D.Sc. (Lond.), and CYRIL WEST, A.R.C.Sc., D.Sc. (Lond.), F.L.S. (With Plate I and 3 Text-figures) . 1
2. Studies in Bacteriosis. III.—A Bacterial Leaf-Spot Disease of *Protea cynaroides*, exhibiting a host reaction of possibly Bacteriolytic Nature. By SYDNEY G. PAINE and H. STANSFIELD. (With Plate II and 4 Text-figures) . 27
3. On the Occurrence of the Immature Stages of Anopheles in London. By FLORENCE E. JARVIS 40
4. The Distribution of Parasite-Infected Fish. By H. CHAS. WILLIAMSON, M.A., D.Sc. (With 4 Text-figures) . . 48
5. Observations on the Habits of Certain Flies, especially of those Breeding in Manure. By J. E. M. MELLOR, B.A. (With 6 Text-figures and 4 Charts) 53

Nos. 2 and 3 (December, 1919)

1. A Phytophthora Rot of Pears and Apples. By H. WORMALD, D.Sc. (Lond.), A.R.C.Sc. (With 2 Text-figures and Plate III) 89
2. Notes on the Biology of *Necrobia ruficollis*, Fabr. [Coleoptera, Cleridae]. By HUGH SCOTT, M.A., Sc.D. (Cantab.). (With 2 Text-figures) 101
3. On the Life-history of "Wireworms" of the Genus *Agriotes*, Esch., with some Notes on that of *Athous haemorrhoidalis*, F. Part I. By A. W. RYMER ROBERTS, M.A. (With 5 Text-figures and Plate IV) 116
4. On a Coenurus in the Rat. By M. TURNER, B.Sc. (With 1 Text-figure) 136
5. Some Factors in Plant Competition. By WINIFRED E. BRENCHLEY, D.Sc. (With 10 Text-figures and Plate V) . 142
6. A Contribution to the Life-history of the Larch Chermes (*Cnaphalodes strobilobius*, Kalt.). By EDWARD R. SPEYER, F.E.S., M.A. (Oxon.). (With Diagram and Plates VI and VII) 171
7. Studies in Bacteriosis. IV.—"Stripe" Disease of Tomato. By SYDNEY G. PAINE and W. F. BEWLEY. (With 5 Text-figures and Plates VIII and IX) 183
8. Notes on the Life-history of *Ephestia kuhniella*. By RAYMOND V. WADSWORTH 203
9. Notes. By J. C. F. FRYER 207
10. Review 210

No. 4 (April, 1920)

PAGE

1. On the Relations between Growth and the Environmental Conditions of Temperature and Bright Sunshine. By Winifred E. Brenchley, D.Sc. (With 13 Text-figures) 211
2. *Glomerella cingulata* (Stoneman) Spauld. and v. Sch. and its Conidial forms, *Glœosporium piperatum* E. and E. and *Colletotrichum nigrum* E. and Hals., on Chillies and *Carica papaya*. By Jehangir Fardunji Dastur, M.Sc. (With Plate X) 245
3. Field Experiments on the Chemotropic Responses of Insects. By A. D. Imms, M.A., D.Sc., and M. A. Husain, B.A. (With 1 Text-figure) 269
4. On Forms of the Hop (*Humulus Lupulus* L. and *H. americanus* Nutt.) Resistant to Mildew (*Sphaerotheca Humuli* (DC.) Burr.). By E. S. Salmon 293
5. On the Sexual Forms of *Aphis saliceti*, Kaltenbach. By Maud D. Haviland 311
6. Proceedings of the Association of Economic Biologists . 314
7. I. The Administrative Problem. By Sir A. D. Hall, K.C.B., F.R.S. 317
8. II. The Training Problem. By Professor V. H. Blackman, Sc.D., F.R.S. 322
9. III. The Agricultural Problem. By E. J. Russell, D.Sc., F.R.S. 326
10. IV. The Horticultural Problem. By F. J. Chittenden, F.L.S., V.M.H. 330
11. V. The Forestry Problem. By Professor W. Somerville, M.A., D.Sc., D.Œc. 333
12. VI. General Discussion 339
13. List of Members of the Association of Economic Biologists for 1920 349
14. Laws of the Association of Economic Biologists . . 355

VOLUME VI SEPTEMBER, 1919 No. 1

PHYSIOLOGICAL PRE-DETERMINATION: THE INFLUENCE OF THE PHYSIOLOGICAL CONDITION OF THE SEED UPON THE COURSE OF SUBSEQUENT GROWTH AND UPON THE YIELD.

V. REVIEW OF LITERATURE. CHAPTER IV.

BY FRANKLIN KIDD, M.A. (CANTAB.), D.Sc. (LOND.),
Fellow of St John's College, Cambridge,

AND

CYRIL WEST, A.R.C.Sc., D.Sc. (LOND.), F.L.S.
(*Imperial College of Science and Technology*).

(With Plate I.)

PAGE
Chapter IV. The Effect of Conditions During Germination and in the Early Seedling Stage upon Subsequent Growth and Final Yield 1
Introduction 1
Physical Treatments of the Seed:
- (*a*) High Temperatures 3
- (*b*) Low Temperatures 6
- (*c*) Electrical Discharge 9
- (*d*) X-Rays 12

Chemical Treatments of the Seed which do not obviously affect its Nutrition:
- (*a*) Acids 13
- (*b*) Chemical Agents other than Acids
  - i. $CuSO_4$ 17
  - ii. Other Salts 20
  - iii. H_2O_2 22

Conclusions 22

CHAPTER IV

THE EFFECT OF CONDITIONS DURING GERMINATION AND IN THE EARLY SEEDLING STAGE UPON SUBSEQUENT GROWTH AND FINAL YIELD.

INTRODUCTION.

IN the previous chapter of this review we (18) dealt with seed-treatments which could be classed as treatments affecting nutrition. The predetermining effect of increased or decreased nutritional supply operating for a limited period during the critical stages of early development was demonstrated. The proportionality established between seedling weights due to differential nutrition is maintained when the nutritional supply is subsequently equalised during the main period of growth, and it is directly reflected in the final yield.

In the light of evidence afforded by growth curves based on dry-weight measurements which were available in the literature, growth and development within the limits of hereditary potentialities were treated as fundamentally matters of physiological pre-determination. The general expression covering growth was described as the Compound Interest Law of Development. The operation of this law may be subject to a number of secondary modifications.

A few fundamental principles are necessary for the study of growth and development. These are conspicuous by their absence in existing text-books of plant physiology, which excel in the assemblage of interesting curiosities and of uncorrelated details. The phenomena of *normal growth* seem to call for further study and analysis and for the application of mathematical treatment. Even a clear grasp of the general conception of the compound interest law of development at once greatly simplifies the handling of problems of physiological pre-determination and of growth. One is able to formulate approximately the magnitude of effects that will be observed as the result of causes operating continuously or for a short time in relation to the stage of development at which the cause operates and the effect is desired.

In the cases with which we dealt in the preceding chapter the absolute magnitude of the final effects upon yield were out of all proportion to the absolute magnitude of the causes to which they were due. These causes operated for a short period during the early stages of development and initiated what we have termed physiological pre-determination. It is this fact which makes the phenomenon of physiological pre-determination of such importance from the economic point of view. Roughly speaking, the absolute value of the effect produced is proportional, not to the value of the initial cause (*i.e.* that which has to be supplied by the agriculturist), but to the value of the initial cause multiplied by the time-interval between the operation of the cause and the reaping of the result.

In the present chapter we deal with seed-treatments which we have classified for convenience under the following headings, viz.:

(1) Physical treatments of the seed;

(2) Chemical treatments of the seed, which do not obviously affect its nutrition[1].

---

[1] It should be pointed out that there are many papers which deal with the effect upon *germination* of various chemical treatments of seeds, but in which no mention is made of the pre-determining effects of the seed-treatments (cf. Bokorny (4); Sigmund (32)).

PHYSICAL TREATMENTS OF THE SEED.

(*a*) High Temperatures.

Experimental work in which seeds in the air-dry condition have been submitted to high temperatures falls into three categories.

It has been established that in the case of many seeds the capacity for germination, though low after the harvest, increases during storage to its full value, which is attained by the following spring. A typical example of the results obtained by Atterberg (2) in the case of barley is given below (Table I).

Table I.

Barley reaped at four stages.

Stage of maturity of the seed when harvested at the end of September	Percentage of Moisture in the seed		Percentage of germination when sown on						
	When reaped at the end of September	On the 20th of October, after having been stored in a cold barn and then taken to the laboratory	Sept. 26th	Oct. 5th	Oct. 20th	Oct. 27th	Nov. 3rd	Nov. 19th	Dec. 2nd
Green	42	19·0	21	6	1	29	45	82	95
Green	39	18·6	17	3	2	31	36	85	94
Yellow ripe	35	18·3	17	2	0	21	30	90	98
Ripe	27	18·4	11	1	4	3	21	85	98

It has been shown by numerous workers (*e.g.* Hotter (16); Velten (36); Atterberg (2), and others) that if the seeds are exposed for a short time to relatively high temperatures during the period of low germination they at once attain their full capacity for germination (cf. Table II).

Table II (after Atterberg).

Kind of seed	Treatment of the seed	Result of germination test
Barley	Dried for 2 days at 37° C.	Gave 22 % germination in 4 days
	,, 4 ,, ,,	,, 50 % ,, ,, 12 ,,
	,, 6 ,, ,,	,, 98 % ,, ,, 10 ,,
	,, 8 ,, ,,	,, 99·5 % ,, ,, 8 ,,
	The control seed (untreated) gave only 4 % germination	

We have here a definite experimental result, but a full explanation of the underlying causes of the change which occurs during storage and which is accelerated by heat is as yet not forthcoming, neither, so far as we have been able to find, are there any records extant as to the influence, if any, this procedure exercises upon the development and final yield of the plants produced.

In the second category we have a large amount of experimental work which has been undertaken with the object of obtaining a simple method of sterilising seeds. In this work tests of the growth and yield of the plants from treated seeds as compared with that of the controls from untreated seeds have been carried out, but in considering the yields obtained the authors have not distinguished between the specific physiological effects of the heat-treatment and the effect of seed sterilisation.

Finally we have a category into which fall experiments carried out with the definite object of ascertaining the pre-determining effect upon growth and yield of exposing seeds to relatively high temperatures (cf. Sprengel (33); Ockel (25); Pietrusky (27); Krašan (21); Velten (36); and Wollny (43 & 44)). The results obtained are contradictory, and no definite conclusion can be drawn from them.

The most striking of the earlier results appear to have been obtained with flax by Pietrusky. A brief exposure of the air-dry seed to temperatures ranging from 30° to 50° C. increased the quality and yield of the fibre produced by the experimental plants.

Wollny (43 & 44) in the case of a number of cereals and other economic crops reached the conclusion that dry heating the seed generally increased the productivity of the plants produced. Some of the results obtained by Wollny are summarised in the following tables (Tables III and IV):

TABLE III (after Wollny).

Experiments carried out in 1876.

Kind of seed	Number of seeds	Weight of the experimental seeds		Percentage loss in weight during the drying-process	Weight of the untreated seeds	Temperature maintained during the drying-process
		on April 5th	on April 30th			
White lupins	200	82·49 gm.	80·07 gm.	2·93	83·30 gm.	30°–35° C.
Peas	200	68·23	64·75	5·10	67·80	30°–35° C.
Flax	—	100	96·95	3·05	99·30	30°–35° C.

Harvest Results.

Kind of seed	Condition of seed sown	Percentage of plants at the harvest	Yield from 100 plants	
			Seeds	Straw
Lupin	Dried at 30°–35° C.	87	371 gm.	406 gm.
	Untreated	95	264	347
Peas	Dried at 30°–35° C.	75	1381	1594
	Untreated	91	1143	1410

			Yield per 4 sq. m.	
			Seeds	Fibre
Flax	Dried at 30°–35° C.	—	290 gm.	1595 gm.
	Untreated	—	222	1208

The area allowed for each plant was 25 sq. cm. in the case of the lupins and peas. The flax seed was sown broadcast over an area of 4 sq. metres. All seed was sown on May 4th.

TABLE IV (after Wollny).

Experiments carried out in 1876–77.

Kind of seed	Number of seeds	Weight of the experimental seeds		Percentage loss in weight during the drying-process	Weight of the untreated seeds	Temperature maintained during the drying-process
		Before drying	After drying			
Winter rye	100	4·79 gm.	4·49 gm.	6·25	4·79 gm.	30°–35° C.
Maize	75	36·40	34·93	4·04	36·40	30°–35° C.
Peas	100	40·77	38·44	5·71	41·61	30°–35° C.
Lupin	100	44·51	42·25	5·08	45·08	30°–35° C.
Flax	—	80·00	76·39	4·52	79·85	30°–35° C.

Harvest Results.

Kind of seed	Condition of the seed sown	Percentage of plants at the harvest	Number of haulms per 100 plants	Yield from 100 plants	
				Seed	Straw
Winter rye	Dried at 30°–35° C.	82	693	1091 gm.	2378 gm.
	Untreated	85	497	808	1412
Peas	Dried at 30°–35° C.	50	—	1638	3125
	Untreated	99	—	1522	2714
Lupin	Dried at 30°–35° C.	83	—	1153	3172
	Untreated	91	—	1519	4304

			Yield from 100 plants	
			Green	Air-dry
Maize	Dried at 30°–35° C.	38	111,250 gm.	74,166 gm.
	Untreated	47	94,000	63,000

		Yield per 4 sq. metres			Weight of 500 of the harvested seeds
		Seeds	Total weight	Chaff	
Flax	Dried at 30°–35° C.	283 gm.	955 gm.	238 gm.	2·20 gm.
	Untreated	341	832	236	2·27

The area allowed for each plant was 20 sq. cm. in the case of the rye, and 25 sq. cm. in the case of the maize, peas, and lupins. The flax was sown broadcast. The seed was sown on May 4th, 1877, with the exception of the winter rye, which was sown on September 22nd, 1876.

An analysis of the effect of this treatment of the seed upon the development of the plant was carried out subsequently in considerable detail by Wollny (44), who showed that (1) the percentage of germination was decreased in some cases (*e.g.* peas, beans, rye), in others (*e.g.* wheat, barley, oats) not appreciably; (2) the growth of the resulting plant was at first delayed; and (3) the experimental plants flowered earlier and more freely than the controls. He also found that seeds after dry heating were unusually sensitive to climatic and soil conditions during germination. As a result of this growth-analysis Wollny appears to have been doubtful as to the utility from the economic point of view of drying seeds.

(*b*) LOW TEMPERATURES.

Many authors have dealt with the effect upon germination of exposing seeds in the moist condition to low temperatures. This has been found to be a method of general application for stimulating the germination of dormant seeds (cf. Kinzel (20)).

The question as to what effect exposure to low temperatures during the critical stages of germination may have upon the subsequent course of development has been investigated in the case of seeds of the so-called winter-cereals which normally germinate in late autumn, pass the winter in the vegetative condition, and flower during the following summer. If the seeds are sown in the spring, the plants produced do not complete their development during the ensuing summer and autumn but they flower and set seed only in the following summer.

This behaviour on the part of winter-annuals has attracted attention in relation to problems of rhythm and periodicity, the question at issue being whether rhythm and periodicity in plants are inherent properties of the protoplasm or the direct effects of external conditions. Without entering into a discussion of the theories put forward by various authors we may deal fully with the careful series of experiments recently carried out by Gassner (10)[1] at Hamburg, and published last year. Gassner planted several winter varieties of cereals[2] in the spring and investigated whether exposure of the seeds during germination or of the plants during the early stages of seedling growth to low temperatures would affect their subsequent development. In the only communication at present available this author confines his attention to the time of formation of the flowering stems (culms) of the cereals investigated.

In each experiment four lots of 50 seeds ("pure line") were germinated on moist sand in crystallising dishes, which were kept at temperatures of 1°–2° C., 5°–6° C., 12° C., and 24° C. respectively. When germination was complete (*i.e.* when the cotyledon had attained a length of from 2 to 2·5 cms.) the seedlings were rinsed with water to remove sand, and the 20 most vigorous were forthwith planted out in four large flower-pots filled with good compost. After one day, during which they were kept in the shade, these flower-pots were sunk in the ground in a part of the Botanic Gardens where uniform illumination was assured, and from the time of germination onwards the plants were grown under similar external conditions.

---

[1] Gassner gives a full list of references to previous work on this subject.

[2] For example, "Petkuser" winter rye; "Friedrichswerther Mammuth" winter barley; "Svalöfs Extra Squarehead" winter wheat, etc.

Curves *A* and *B* in Fig. 1 give the temperatures obtaining at 1 p.m. and at 7 a.m. respectively from March 1st to September 30th. The time of flower-stem formation was reckoned from the day on which at least one flower-spike of a plant in a series had emerged at least half-way from its surrounding leaf-sheath.

His results may be briefly summarised as follows. Exposure of the seeds to low temperatures during germination or during the early seedling stage ensures that flowering shall occur during the first year (Plate I, Fig. I; and cf. Appel and Gassner(1)). He carried the analysis further and obtained the following quantitative results. Firstly, the lower the temperature (over a range of 0°–25° C.) the shorter the interval between germination and culm-formation as is shown in Fig. 2, which we have constructed from Gassner's data. Secondly, the earlier in the development of the plant the exposure to the low temperature occurs, the more marked the result (see Tables V and VI; and cf. Gassner(9)).

TABLE V.

Effect of a low temperature at different stages in the development of "Petkuser" winter rye.

Date of sowing	Treatment following the sowing		Date on which the seedlings were planted out*	Result
March 18th	A. Kept at 24° C. for 30 hours	Followed by a temperature of 1°–2° C. for 4 weeks	April 16th	Formed flowering-stems irregularly from the beginning of August
	B. Kept at 1°–2° C. for 4 weeks	Followed by a temperature of 24° C. for 30 hours		Formed flowering-stems regularly from June 25th onwards

* On April 16th the cotyledons of the plants belonging to series A were about 20 mm. in length whereas those belonging to series B were about 30 mm. in length.

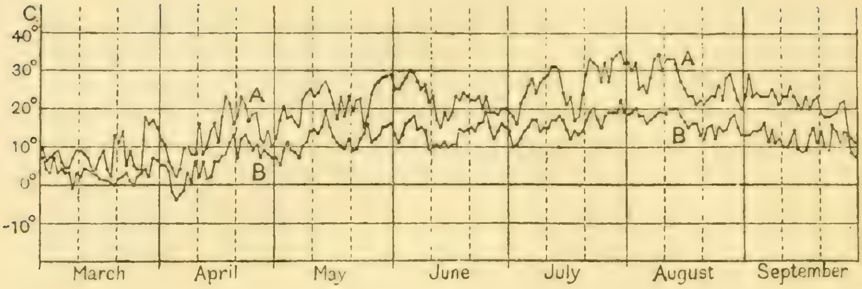
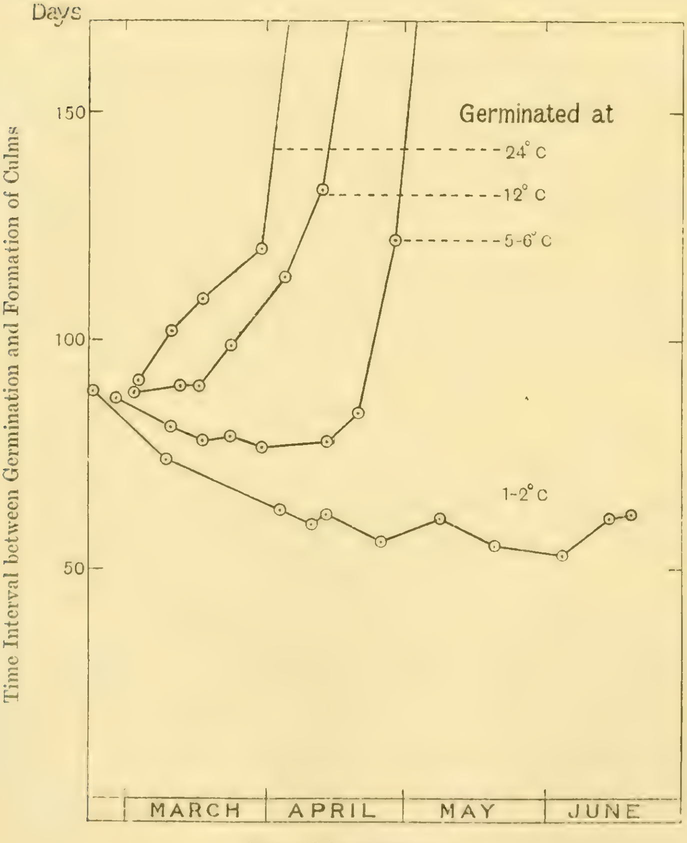


Fig. 1.



Date of Germination

Fig. 2.

TABLE VI.

Effect of a low temperature at different stages in the development of "Uruguay" oats.

	Treatment	Result of treatment
Seeds kept at 6°–9° C. for 5 days	Followed by a temperature of 25° C. until germination was completed	Plants flowered during the same season
Seeds kept at 25° C. for 1–2 days	Followed by a temperature of 6°–9° C. for 5–7 days (*i.e.* until germination was completed)	Plants did not flower during the same season

If the exposure to the low temperature occurs 2–3 days after sowing at normal temperatures (*e.g.* 24° C.) it is necessary that the period of exposure to the low temperature be many times as long in order to obtain the same result as when the exposure is made during the first few hours after sowing (see Table VII).

TABLE VII.

Influence of low temperature on the time of culm-formation in "Petkuser" winter rye sown in the spring.

Treatment		
Germination period at 24° C.	Followed by a period at 0° to −5° C.*	Result of the treatment
3 days	25 days	Formed flowering-stems the same year after 68 days
3 ,,	3 ,,	Did not form flowering-stems the same year
3 ,,	1 ,,	
3 ,,	0 ,,	

* The plants were subsequently grown under natural conditions.

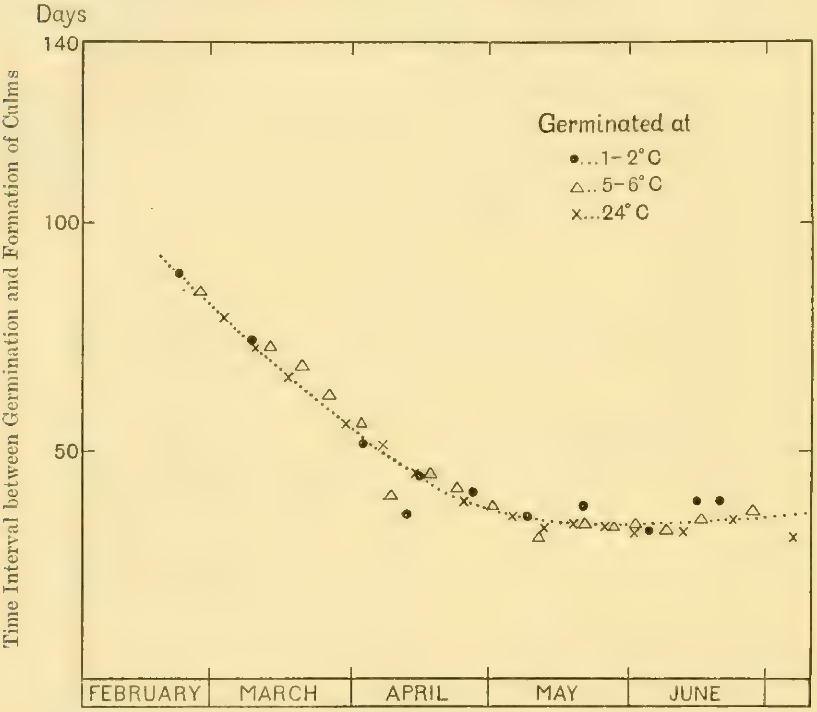
In parallel experiments carried out with so-called summer-annuals of the same varieties it was found that exposure to low temperatures during germination did not appreciably influence the time at which culm-formation took place[1] (see Fig. 3).

(*c*) ELECTRICAL DISCHARGE.

Results of empirical experiments dealing with the effects of electrical discharge upon seeds during germination are on record. The interesting aspect of these experiments from our point of view lies in the fact that it is stated that brief exposure of seeds prior to and during germination influences not only the vigour and percentage of germination, but also the whole course of subsequent growth and final yield. It is interesting in this connection to note the fact that from the records of experiments in which growing crops have been submitted to electrical discharge throughout their development there is reason to believe that beneficial results are most obvious during the initial stages of growth.

---

[1] Gassner and Grimme (11) have shown that plants which require a period of low temperature to bring about complete development, can withstand extreme cold, whereas plants which do not need a low temperature, are unable to withstand cold.



Date of Germination

Fig. 3.

The following table (Table VIII) summarises certain recent results obtained at the Research Station for Plant Physiology at Dahlem, which were reported by Höstermann (15) in the *Landwirthschaftliche Jahrbücher* for 1913. The main significance of these results, apart from the fact that effects were found to last throughout the life of the plant, seems to be that better results are obtained when the seeds are treated after swelling in water than when treated dry, and that injury can easily result from too powerful a discharge.

Table VIII.

A. *Experiments with Seeds as the Positive Electrode.*

Kind of seed used and its condition during experiment	Distance of discharging electrode from the seeds	Length of spark	Duration of discharge	Effect of treatments upon germination and subsequent growth
Dry seeds of *Phleum pratense* sown in germination dishes	5 cm.	22 mm.	1 min.	Has a *favourable* influence upon germination and also upon the subsequent growth
		32 mm.		Has an *unfavourable* influence upon the later growth
Swollen seeds of *Phleum pratense* sown in germination dishes	5 cm.	12 mm.	1 min.	The germination power is *greatly decreased* probably because the seeds were swollen for too long a period and because the discharge was too intense
Dry seed of Spring Rye sown in germination dishes	5 cm.	12 mm.	1 min.	No effect
			2 mins.	These treatments have an initial *favourable* action upon germination and produce a *final small increase in growth*
			3 ,,	
			5 ,,	
			10 ,,	Causes injury and delay in growth

B. *Experiments with Seeds as the Negative Electrode.*

Kind of seed used and its condition during experiment	Distance of discharging electrode from the seeds	Length of spark	Duration of discharge	Effect of treatments upon germination and subsequent growth
Dry seeds of Spring Rye sown in germination dishes	40–50 cm.	40 mm.	½ hour	Result in an *increase of germination* and of *ear-formation*, but a *decrease in growth*
			1 ,,	
			1½ hours	
			2 ,,	
Swollen seeds of Barley; these seeds had been previously soaked in water for 6 hours at 30° C. and were afterwards sown in the open	5 cm.	32 mm.	2 mins.	The effect of these treatments is at first to increase growth considerably, but the difference disappears later
			10 ,,	
			30 ,,	
Swollen seeds of Spring Wheat; these seeds had been previously soaked in water for 6 hours at 30° C. and were afterwards sown in the open	5 cm.	23 mm.	2 mins.	The effect of these treatments is to increase growth; this *increase in growth is maintained.* Ear-formation was doubled by the 10-minute treatment
			10 ,,	
			30 ,,	

Swollen seeds of Spring Wheat; these seeds had been previously soaked in water for 6 hours at 30° C. and were afterwards sown in the open	5 cm.	32 mm.	2 mins. 10 ,, 30 ,,	*Increased growth was obtained* particularly after the 2 minute and 10 minute periods * * This experiment was repeated with similar results
Swollen seeds of Spring Rye; previously soaked in water at 30° C. for: 1 hour 3 hours 5 ,, 6 ,, 7 ,, 8 ,,	10 cm.	32 mm.	15 mins.	The best results upon subsequent growth were obtained with the seeds which had been soaked in water for 6, 7, and 8 hours respectively
Swollen seeds of Spring Rye; soaked in water at 30° C. for 72 hours and then sown in the soil	40 cm.	40 mm.	30 mins.	Resulted in an *increase in germinating power and in growth energy*
Swollen seeds of Spring Wheat; previously soaked for 5 minutes	2 cm. ,, ,,	27 mm. ,, ,,	2 mins. 5 ,, 10 ,,	No acceleration in germination
Placed in germination dishes	,, ,,	,, ,,	20 ,, 30 ,,	*Considerable delay in germination*
Swollen seeds of Spring Wheat; previously soaked for 5 minutes Placed in germination dishes	2 cm. ,, ,, ,, ,, ,,	12 mm. 22 ,, 27 ,, 32 ,, 40 ,, 50 ,,	10 mins. ,, ,, ,, ,, ,,	Results: small acceleration at lower voltages; slight injury at moderate voltages; decided injury at high tensions (*i.e.* with spark lengths of 40 mm. and 50 mm.)

According to Micheels and De Heen (23) the action of a high frequency alternating current upon wheat and pea seeds, which had previously been soaked in water for 24 hours, favourably affected the development of the seedlings, but unfortunately their observations extended over a few days only.

(*d*) X-rays.

Increased vigour of germination and increased growth of the resulting plant, so far as it has been followed, has been recorded by several authors as the result of brief treatment of the seeds to X-rays. An example may be quoted. Promsy and Drevon (31) found that exposure of swollen seeds for ½–1 hour to the influence of X-rays markedly increased the subsequent growth of the seedlings. This action of the X-rays occurred only when the seeds were kept at a relatively high temperature (40° C. *circa*) during the exposure. For details with regard to the rays used and the conditions of exposure, which were carefully recorded by the investigators, reference should be made to the original paper. The following table (Table IX) has been based upon the results obtained by Promsy and Drevon:

TABLE IX.

Experiment I.

White lupin seeds were soaked in water for 15 hours, after which the testas were removed. On the first 3 days the experimental seeds were exposed to the X-rays for 1 hour, ½ hour, and ½ hour respectively, the temperature being 40–45° C. On the 4th day the seeds were sown in damp sand together with the controls (untreated).

Results.

Results on	Treated*	Untreated
4th day	Average length of radicles = 16·7 mm.	Average length of radicles = 6·2 mm.
18th ,,	Shoots appeared	—
26th ,,	—	Shoots appeared
29th ,,	Average height of plants above level of sand = 9·9 cm.	Average height of plants above level of sand = 7·3 cm.

* The treatment also brought about certain anatomical modifications.

Experiment II.

Seeds of haricot beans were soaked in water for 2 hours after which they were exposed to X-rays for 1 hour (temp. 40° C.).

Results.

	Treated	Untreated
Average length of plants on the 15th day	10 cm.	5 cm.
Average dimensions of		
1. Cells of the cortex	55·0 μ	44·0 μ
2. Cells of the pith	48·0 μ	43·0 μ
3. Nuclei of the cortical cells ...	18·0 μ	11·1 μ
4. Nuclei of the pith cells	15·0 μ	13·2 μ

CHEMICAL TREATMENTS OF THE SEED.

(*a*) ACIDS.

A large number of workers (*e.g.* Fischer (8), Onodera (26), and others) have noted the stimulating effect of acids upon germination. We have only been able to find a few cases in which observation was extended to the subsequent course of development of the treated seeds, but whenever this has been done, it is interesting to find that the author has usually recorded favourable results of a more or less striking nature. A few examples may be quoted.

Promsy (30), having first established the fact that the effect upon germination of a continuously-acting acid medium was favourable in a large number of trials, employed the method of soaking the seeds *for a short time* in the acid solutions and then sowing them in garden soil.

Seeds of a variety of *Cucurbita Pepo* were soaked for 48 hours in the following solutions, viz.:

0·5 % Tartaric acid	(*T*)
0·5 % Acetic acid	(*A*)
0·5 % Oxalic acid	(*O*)
Pure water	(*W*)

After this preliminary soaking treatment the seeds were washed in water and were then sown in sand in perforated dishes. *A* came up first, *T* next, followed by *O*, and several days later by *W*. Measurements taken sometime later (*i.e.* when the seedlings bore from 2–6 leaves) showed that the *A* plants had the largest number of leaves and also the greatest dry-weight, whereas the *W* plants had the smallest number of leaves and the smallest dry-weight. Forty days after sowing the perforated dishes were half buried in garden soil, but a single plant from each lot was transplanted. The final results in the case of those not transplanted were as follows. All the *W* plants died; of the others, flowers appeared first upon the *A* plants, and these plants also bore the largest and most numerous fruits. All the plants from the acid-treated seeds maintained their vigour throughout the experiment.

Of the transplanted plants, *A* produced three very large fruits, *O* produced two, *T* produced one, whilst *W* flowered, but did not fruit. Results of a similar nature were obtained by this author with Pepper seeds.

The main interest of these results lies in the fact that a brief treatment during the critical stage of germination was found to produce a beneficial effect on the whole course of subsequent development of the plants and also upon their final yields.

We may recall here the incidental observations of three other workers, namely, Goodspeed, Townsend, and Plate. Goodspeed (12), when testing the effect of 80 per cent. H_2SO_4 upon the germination of tobacco seeds, found that treatment with this acid for a period not exceeding 10 to 12 minutes markedly increased the percentage of germination, and in some cases the rapidity of germination also. This result is in harmony with the results of many other investigators on the effect of strong acids upon the germination of hard-coated seeds. From our point of view, however, Goodspeed's most interesting contribution lies in a sentence hidden in the body of his paper—"Results at present at hand seem to leave no doubt that the action of sulphuric acid is further strikingly effective in increasing the rate of growth during at least the first three months of the plant's life." This observation of Goodspeed's is supported by results recorded by F. Plate (29). Working with seeds of *Avena sativa* Plate noticed that after treatment with various inorganic acids the germination of the seeds was greatly accelerated, and that the plants produced from the treated seeds were more vigorous than the controls. He observed that the reserve materials were exhausted in the case of the acid-treated seeds in 10 days as against 15 days in the case of untreated seeds.

The effect of hydrocyanic acid gas upon dry and moist seeds respectively has been investigated by Townsend (34 and 35); the necessity for the investigation arose from the rapidly increasing use of this gas in the destruction of insect pests infesting stored grains and other seeds and also for the fumigation of greenhouses. Townsend found that *dry* seeds of corn, wheat, beans and clover might remain without injury to their germinating power for several weeks in an atmosphere containing a greater concentration of hydrocyanic acid gas than is required to kill quickly insect life. The germination of these seeds was found to be accelerated after this treatment and the rate of growth of the seedlings to be above the normal.

The action of boric acid upon the germination and subsequent development of seeds has been investigated by Morel (24). This author's results showed that brief treatment with boric acid at the time of germination produced a persistent deleterious effect upon haricot beans. The results noted about 7 weeks after sowing in ordinary soil are given in the following table:

TABLE X.

Treatment of the seeds previous to sowing in soil		
Strength of acid used	Period of soaking	Results noted in the plants after 7–8 weeks' growth
1 % boric acid	15 mins.	Showed no appreciable difference from the controls
1 % ,,	30 ,,	Differed from the controls only in the colour of their leaves which were of a less clear green
1 % ,,	60 ,,	The leaves of these plants were small and yellowish

It is seen that treatment of the *dry* seed with a 1 per cent. solution of boric acid even for ½ hour has a clearly visible effect upon the resulting plant during its whole course of growth.

In a similar series of experiments with seeds which had been previously immersed for 6 hours in water in order to render them more permeable to the acid solution, the following results were obtained:

TABLE XI.

Treatment of the seeds subsequent to the 6 hours soaking in water, but previous to sowing*		Results noted in the plants after about	
Strength of acid used	Period of soaking	5 weeks' growth	7 weeks' growth
1 % solution of boric acid	1 hour	Plants poor, with small yellowish leaves	Growth of plants moderately vigorous, but their leaves remained yellowish and were much smaller than those of the controls
1 % ,,	2 hours	Plants poor, with small yellowish leaves	
1 % ,,	3 ,,	A very few plants came up and these were very feeble	
1 % ,,	6 ,,	Few very feeble etiolated plants produced, leaves very small and few in number	Growth very poor although showing a decided improvement

* The seeds were placed on damp sand for a few days at a favourable temperature and were then sown in garden soil. Only those treated for the shortest period (*i.e.* 1 hour) had germinated after an interval of 3 days.

Similar experiments carried out with wheat gave results analogous to those obtained with haricot beans.

The present authors, working with *Brassica alba*, have shown that concentrations of carbonic acid (19) and boric acid (41) which rapidly kill the growing root, have no injurious effect upon any part of the embryo in the ungerminated but fully swollen seed. We may distinguish three ranges of increasing concentration of these two acids, as follows. (1) A range of low concentration in which the seeds germinate, but suffer injury after germination. (2) A range of intermediate concentration in which the germination of the seeds is inhibited. No injury to any part of the embryo or seedling can be observed even after prolonged treatment with this concentration of acid when the seeds are finally brought to germination in an acid-free medium. In this region marked injury is shown, however, by seeds which are allowed to germinate before being placed in the acid medium. (3) A range of higher concentration in which the seeds suffer injury whether ungerminated or germinated. The concentration of acid used by Morel lies in this third region which causes injury to the ungerminated seed.

This difference between the effect of chemical solutions upon the growing plant and their effect upon the seed before germination is not confined to acids but appears to be general. For instance, Hicks (13 and 14), who tested the effect upon seeds of a number of chemical fertilisers, reached the conclusion that the effect of treating seeds with various chemicals before sowing is no index of the action of these chemicals when applied to the soil. Injury to the young plant may result when the chemicals are applied to the soil although no injurious effect is shown when the seeds are treated before germination with the same solution. However, little can be said on this subject with certainty until it has been determined whether the solute under consideration penetrates the testa or not.

(b) CHEMICAL AGENTS OTHER THAN ACIDS.

(1) *Copper Sulphate* (= *Bluestone*).

We have previously dealt with the effect of soaking seeds in water (18), and have drawn attention to the distinction which must be made between seeds sown wet (*i.e.* immediately after the soaking treatment) and seeds sown after re-drying, with or without storage. It is necessary to bear these points in mind when dealing with the effect of treating seeds with chemical solutions in which they are immersed for various periods.

In 1904 Bréal and Giustiniani (6) published the results of an investigation on the effect of treating the seeds of various cereals with a solution of copper sulphate. Unfortunately, although they appear to have been aware of the distinction which must be made between the effect of soaking and the effect of the solute alone, their results, whilst demonstrating a considerable increase in yield as a result of the treatment they employed, do not allow us to draw any critical conclusion as to how far they are due to the soaking and how far they are due to any specific action of the copper.

Their line of thought appears to have been as follows: Seeds sown after being allowed to take up moisture are found to give a greater yield, but damp seeds are very susceptible to fungal attack. Copper sulphate, however, has frequently been employed as a fungicide in seed-treatments. Hence, can seeds be soaked in a solution of copper sulphate, not only without injury, but with a result beneficial to yield? Further, might it not be advantageous to make up the copper sulphate solution together with 2–3 per cent. of starch, on the grounds that by so doing the escape of soluble food-materials from the seed into the surrounding medium during the period of soaking would probably be decreased[1]? They therefore adopted a Copper-Starch soaking treatment followed by liming and re-drying, and record results from which it appears that this treatment of the seeds renders them more resistant to fungal attack without affecting their germinating capacity. Moreover, seeds thus treated give rise to plants which are better developed and produce a larger yield than plants from untreated seeds. Bréal and Giustiniani drew attention to the fact that from the very beginning of their development the plants from the treated seeds gained on the controls, and that the superiority of the yield from the experimental plants over that from the controls was most marked in the case of the "heads." In the two following tables (Tables XII and XIII) the results of the authors' experiments are summarised, but these results, although of general economic interest, are unsatisfactory from our point of view because they do not show conclusively that the copper sulphate has any specific action on the seeds. Taken in conjunction with the beneficial results obtained by simply soaking cereal seeds in water, and in conjunction with the harmful effects of copper-treatments upon seeds recorded by other authors, it seems probable that the improvement of the plants following the copper-starch treatment of the seeds is to be attributed to the soaking alone.

---

[1] We have not found any published evidence to the effect that starch does decrease the exosmosis of soluble food-materials from the seed.

TABLE XII.

Pot-culture experiment with equal weights of treated and untreated seed.

For details of the seed-treatments the original paper should be consulted.

Kind of seed	Duration of culture in days	Weight of the aerial parts of plants from treated seed, that of the control plants being taken as 100
Maize "Quarantain"	65	160
Wheat "Chiddam"	38	122
Barley "Chevalier"	36	120
Oats	35	110
White Lupin	33	119
Buckwheat	30	116

In a later investigation Bréal(5) confirmed his previous results and also conducted a number of water-culture experiments with treated and untreated seeds respectively of wheat, oats, barley and maize. These seeds were sown in vessels containing pure water, and the dry weight of the seedlings was taken after various short periods (*i.e.* 25–52 days). It was found (Table XIV) that in each case the total dry weight of the seedlings at the end of the experiment was less than that of the seeds originally sown, but that the plants from the treated seeds weighed considerably more than those from the untreated, this result being due to the more vigorous stem and leaf development of the experimental plants. The results also show that the superiority of the plants from the treated seeds is evident from the beginning of their development.

TABLE XIII.

Experiments with equal weights of treated and untreated seeds sown "en pleine terre."

Maize seed used in each experiment.

No. of expt	Seeds	Fresh weight in kilograms after 100 days' growth		Weight of the aerial parts of the plants from treated seeds, that of the control plants being taken as 100	
		Entire yield	Heads	Entire yield	Heads
I	Treated	0·765	0·270	137	146
	Control	0·565	0·185		
II	Treated	3·100	0·920	120	129
	Control	2·500	0·710		
III	Treated	4·200	1·295	107	148
	Control	3·900	0·870		
IV	Treated	2·000	0·615	74	112
	Control	2·700	0·545		
V	Treated	4·000	0·605	114	121
	Control	3·500	0·500		

TABLE XIV.

Kind of seed	Duration of experiment in days	Dry weight in grams of the seeds sown	Dry weight in grams of yield from		% difference in yield in favour of the plants from treated seeds
			Untreated seeds	Treated seeds	
Wheat "Bordeaux"	25	88	60	72	20
,, ,,	52	88	45	66	46
Wheat "Dattel"	20	87	77	81	5
,, ,,	40	87	65	75	15
Wheat "Japhet"	20	89	77	80	4
,, ,,	40	89	60	67	11
Wheat "Bordier"	23	87	74	76	2
,, ,,	37	87	60	69	15
Wheat "Saumur"	20	88	75	83	10
Oats "Houdan"	27	87	70	78	11
Oats "Brie"	28	89	67	82	7
Barley	23	90	62	70	14
Maize "Gros jaune"	50	89	72	80	11
Maize "Dent de cheval"	32	89	73	81	10

Beyond the really important fact thus brought out that the final result can be forecasted at a very early stage in the development of the seedling, it is impossible on the basis of the data given to determine the factors responsible for the results obtained. Bréal, however, is satisfied to conclude that the treatment ensures a better utilisation of the seed-reserves.

In view of the results obtained by Bréal and Giustiniani, which, as we have pointed out, cannot be attributed in the absence of further evidence to the specific action of the copper, the recent critical work of Jungelson (17), who worked with maize, is of interest. Jungelson used simple solutions of various copper salts and obtained similar results whatever the nature of the anion, thus definitely indicating that copper is the main factor in producing the results. He also showed that the results varied with the concentration of the salt.

The effects of the copper treatment on the seeds showed themselves throughout the whole course of development and were even carried over into succeeding generations. These effects, however, although very distinct and characteristic, were altogether harmful from the point of view of vigour and yield. Firstly, the copper treatment of the seeds decreases their power of germination, and secondly, there is both a retardation of the vegetative development and a delay in the flowering of the plants produced. Thirdly, a tendency towards variation, which manifests itself in the appearance of abnormal "heads" and seeds, is shown by the plants from the treated seeds; but these new characters do not appear to be handed on to the next generation. Lastly, plants from seeds treated in identically the same way exhibit totally different abnormalities.

Jungelson's results are especially important from two points of view; firstly, they demonstrate the persistence of the effect of the copper treatment of the seeds, and secondly they prove that the results of treating seeds with copper are distinctly unsatisfactory. Jungelson himself suggests that the degeneration of local races of cereals, which has become so marked of late years, may in a certain measure be due to the general use of seed-treatments in which copper is employed for the purpose of preventing the development of smut.

(II) *Other salts.*

We have already indicated the possibility that such results as those obtained by Bréal and Giustiniani (6) may be due to the soaking involved in their treatment of the seed rather than to the action of the copper. This possibility must be borne in mind when the question of other seed-treatments which involve soaking for certain periods in solutions of various salts is under consideration.

Accounts of the treatment of seeds with solutions of various salts with the object of testing the effect upon final yield are to be found scattered through the literature, but although sweeping conclusions are occasionally drawn, the experimental data upon which these conclusions are based are in the majority of cases completely inadequate. Two or three examples may be given.

In discussing the results of a long series of pot-culture experiments extending over a number of years, carried out at the Woburn Experiment Station with the primary object of testing the manurial value of small quantities of the so-called rarer constituents of ash, Voelcker (40) observes (p. 325) that "certain metallic salts have either a toxic or a stimulating effect upon vegetation, the particular effect depending upon the quantity of the metal present. At what stage of the plant's life are these influences exerted? The evidence so far adduced, leads strongly to the belief that it is during the germination of the seed, rather than at the later stages of the plant's growth, that these influences are exercised."

The substances tested by Voelcker were in most cases applied to the soil, but in a few experiments the only application of the substances was to the seeds, which were soaked in solutions for a short time before sowing. It was found that in some cases this treatment gave very favourable results, and in other cases it produced a moderately good result, whereas when the same substances were applied to the soil in various amounts, the results obtained were always negative. Some of the results obtained by Voelcker (37, 38, 39, and 40) are collected together in the following table (Table XV).

TABLE XV.

	Treatment*		Yield result expressed as % increase or decrease as compared with the control	
Kind of seed used	Solution used	Period of soaking	Grain	Straw
Winter Wheat (White Chaff Browick)	1 % NaI	10 mins.	+16·5	+30·1
	1 % NaBr	10 ,,	+ 8·7	+10·0
Wheat	10 % MnI	15 ,,	−30·9	− 4·5
	5 % MnI	15 ,,	− 0·4	+ 3·4
	1 % MnI	15 ,,	+ 3·1	+13·3
Barley	10 % NaBr	10 ,,	+13·8	+19·6
	10 % MnI	15 ,,	+12·7	+14·2
	5 % MnI	15 ,,	+ 5·6	+ 8·5
	1 % MnI	15 ,,	+14·2	+13·0

N.B. In a later series of experiments it was found that soaking the seed for 20 mins. in NaI or NaBr (1, 10, and 20 % solutions) did not give beneficial results.

* All the seeds were steeped in hot water for 10–15 minutes before treatment in order to kill smut.

These results should be accepted with considerable reserve since the pot-culture experiments were conducted with relatively few plants and the probable errors of the experiments were not determined.

A regular increase in yield with increased strength of the solution employed was reported by J. Craig (7) as the result of soaking pea seeds for one hour in solutions of $NaNO_3$ of the following concentrations, viz. 1 oz., 2 oz. and 3 oz. of the salt to one gallon of water.

One more instance may be noted. An increase in the tillering of several varieties of wheat to the extent of 12·8 per cent. and 20·6 per cent. respectively as the result of treating the seed with $(NH_4)_2SO_4$ (3 per cent. solution) and NH_4NO_3 (3 per cent. solution) was recorded by Wild (42) in the *Agricultural Journal of New Zealand*, 1914. In order to estimate the tillering 20 plants were taken at random from the various experimental plots, and in the case of each variety tested it was found that the effect of the treatment upon the tillering of the plants was a positive one. But here again the experimental data upon which the conclusions were based appear to be totally inadequate.

(III) *Hydrogen peroxide.*

Several workers have recorded observations on the effect of hydrogen peroxide treatments of seeds upon germination and upon the seedlings produced from the treated seeds. It would appear that in some cases hydrogen peroxide in certain concentrations may stimulate germination (cf. Pinoy and Magrou (28)), but the usual effect recorded is a retardation of the germination of the seeds.

Massee (22) when testing the effect of hydrogen peroxide upon seeds with a view to its possible utilisation in seed-sterilisation found that although germination was retarded, the growth of the seedlings eventually produced was rapid so that in many cases at the end of three weeks the plants from the treated seeds were distinctly larger than those from untreated seeds used as controls. But unfortunately the records of investigations with hydrogen peroxide are usually completely unsatisfactory for the reason that the strength of the solution employed is not determined.

CONCLUSIONS.

In concluding this review of the literature bearing upon what we have termed physiological pre-determination we may briefly summarise the available evidence. The evidence, as a whole, seems to show that the factors which influence the plant during its earliest stages of development, have a more or less pronounced effect upon the whole of its subsequent life-history.

In the first chapter of this review we dealt with the factors which acted upon the plant whilst still a seed upon the parent. The most useful criterion here was found to be the size of the seed. A large amount of work bearing upon the effect of the size of the seed upon the growth and yield of the plant produced was reviewed, and an endeavour was made to distinguish critically between genetic and physiological factors. A certain amount of evidence was found indicating that the effects of the parental environment of a seed were sometimes only visible in the resulting plant.

In chapter II we dealt with the influence of the degree of maturity of the seed at the time of harvesting upon its "potentiality," and came to the conclusion that all comparisons made between mature and immature seeds were vitiated by the fact that immature seeds deteriorate more rapidly under storage conditions than mature seeds. In many cases it was found that the yield per plant from immature seed was at least equal to that from mature seed.

In the third and present chapters we have dealt with the aspect of the subject which is probably of most interest to the practical man, namely, the effect of the conditions during germination and in the early seedling stage upon subsequent growth and final yield. The work dealing with the soaking of the seed in water or salt solutions was critically reviewed in chapter III. In the present chapter the most interesting group of facts which have come under review appear to be those brought out by the work of Gassner and others on the effect of low temperatures in pre-determining the time of flowering of spring-sown winter cereals. This effect of exposure to low temperatures is a very clear and distinct phenomenon. While it still remains unexplained, it nevertheless bears out the general thesis based on the evidence which we have collected from various sources, namely, that the external conditions which obtain during the early stages of the development of the plant have a very pronounced effect upon its subsequent development. The results of Gassner's investigations show clearly that it is during the first few hours of germination that the "pre-determination phenomenon" can be most easily and quickly brought about by exposure to cold. As the seedling develops, the duration of the exposure to cold and the degree of cold necessary to ensure flowering in the same year rapidly increase.

While much is known with regard to the effect upon germination of various chemical treatments of seeds, very little experimental work is on record with regard to the subsequent growth and yield of the plants produced from the treated seeds. All the available evidence, however, supports the conclusion that where germination and early seedling growth are stimulated by chemical treatments of the seed the subsequent growth and final yield are favourably influenced in proportion.

One of the most interesting outcomes of the present review of literature has been to emphasize the fact that normal plant-growth falls into line with a "compound interest" law of development. The data obtained by various workers from growth experiments with plants from seeds which had been deprived of part of their original food-reserves show that, broadly speaking, the growth and yield of the resulting plants are proportional to their initial "food-capital," and thus provide an illuminating demonstration of this "compound interest" law.

BIBLIOGRAPHY.

(1) Appel, O. und Gassner, G. Der schädliche Einfluss zu hoher Keimungstemperaturen auf die spätere Entwicklung von Getreidepflanzen. *Mitteil. aus d. Kais. Biolog. Anst.* and *Land- und Forstwirtschaft*, Heft 4, 1907, p. 5.

(2) Atterberg, A. Die Nachreife des Getreides. *Landw. Versuchs-St.* 67, 1907, p. 129.

(3) Babcock, S. M. Metabolic Water: Its Production and Rôle in Vital Phenomena. *Univ. of Wisconsin Agric. Expt. Sta., Research Bull.* No. 22, March, 1912.

(4) Bokorny, T. Ueber den Einfluss verschiedener Substanzen auf die Keimung der Pflanzensamen: I, II and III. *Biochem. Zeitschr.* 50, 1913.

(5) Bréal, E. Traitement Cuivrique des Semences. *C. R. de l'Acad. des Sc.* Paris, 142, 1906, p. 904.

(6) —— et Giustiniani, E. Sur un Nouveau Traitement des Semences. *C.R. de l'Acad. des Sc.* Paris, 139, 1904, p. 554.

(7) Craig, J. Rpt. of the Horticulturist. *Canada Expt Farms Rpt.*, 1897.

(8) Fischer, A. Wasserstoff- und Hydroxylionen als Keimungsreize. *Ber. d. Deutsch. Bot. Ges.* 25, 1907, p. 108.

(9) Gassner, G. Beobachtungen und Versuche über den Anbau und die Entwicklung von Getreidepflanzen im subtropischen Klima. *Jahresber. d. Vereinig. f. Angew. Bot.* 8, 1910, p. 95.

(10) —— Beiträge zur physiologischen Charakteristik sommer- und winterannueller Gewächse, inbesondere der Getreidepflanzen. *Zeitschr. für Bot.* 10, 1918, p. 417.

(11) —— und Grimme, C. Beiträge zur Frage der Frosthärte der Getreidepflanzen. *Ber. d. Deutsch. Bot. Ges.* 31, 1913, p. 507.

(12) Goodspeed, T. H. Notes on the Germination of Tobacco Seed. *Univ. of California Publications in Botany,* v, No. 5, 1913, pp. 199–222.

(13) HICKS, G. H. The Effect of Fertilizers on the Germination of Seeds. *Proc. Amer. Assoc. Advanc. Sc.* 47, 1898, p. 428.

(14) —— The Germination of Seeds as Affected by Certain Chemical Fertilizers. *U. S. Dept. Agric. Bot. Bull.* 24, 1900.

(15) HÖSTERMANN. Versuche über die Beeinflussung des Erntenutzungswertes durch die "Elektrokultur." *Landw. Jahrb.* 45, I, 1913, p. 77.

(16) HOTTER, E. Ueber die Vorgänge bei der Nachreife von Weizen. *Landw. Versuchs-St.* 40, 1892, p. 356.

(17) JUNGELSON, A. Sur des Épis anormaux de Maïs obtenus à la suite du Traitement Cuivrique de la Semence. *Rev. gén. de Bot.* 29, Nos. 344 and 345, 1917.

(18) KIDD, F. and WEST, C. Physiological Pre-Determination: The Influence of the Physiological Condition of the Seed upon the Course of Subsequent Growth and upon the Yield. IV. Review of Literature. Chapter III. *Ann. Appl. Biol.* 5, 1919, p. 220.

(19) —— The Controlling Influence of Carbon Dioxide. Part IV. On the Production of Secondary Dormancy in Seeds of *Brassica alba* following Treatment with Carbon Dioxide, and the Relation of this Phenomenon to the Question of Stimuli in Growth Processes. *Ann. of Bot.* 31, 1917, p. 457.

(20) KINZEL, W. Frost und Licht als beeinflussende Kräfte bei der Samenkeimung, etc. Stuttgart, 1913.

(21) KRAŠAN, F. Beiträge zur Physiologie der Pflanzen. *Sitzungsber. d. Kais. Akad. d. Wiss. math.-naturwiss. Cl.* Wien, 68, I Abt. 1874, p. 195.

(22) MASSEE, I. The Sterilization of Seed. *Journ. Board of Agriculture* (Lond.), 20, 1913–1914, p. 796. Also in *Kew Bull.* 5, 1913, p. 183.

(23) MICHEELS, H. et DE HEEN, P. Action des Courants Alternatifs de Haute Fréquence sur la Germination. *Bull. de l'Acad. Roy. de Belgique* (*Cl. des Sc.*), 1908, p. 82.

(24) MOREL, J. Action de l'Acide Borique sur la Germination. *C. R. de l'Acad. des Sc.* (Paris), 114, 1892, p. 131.

(25) OCKEL, E. *Bericht über das Versuchsfeld Frankenfelde*, Berlin, 1854, p. 147.

(26) ONODERA, I. Untersuchungen über die Beschädigung der Pflanzen durch Säuren und über die Reizwirkungen der Säuren auf Pflanzen. *Ber. d. Ōhara Inst. f. landw. Forsch.* 1, I, 1916, p. 53.

(27) PIETRUSKY. Versuch mit gedörrtem Leinsamen. *Landw. Jahrb.* 2, 1873, p. 138.

(28) PINOY et MAGROU. Sur la Stérilisation des Graines. *Bull. de la Soc. Bot. de France*, 59, 1912, p. 609.

(29) PLATE, F. Ricerche sui fenomeni d' imbibizione dei semi di *Avena sativa*. *Atti della Reale Acad. dei Lincei Rendiconti*, 22, 1913, p. 133.

(30) PROMSY, G. *Du Rôle des Acides dans la Germination.* Marseille, 1912.

(31) —— et DREVON, P. Influence des Rayons X sur la Germination. *Rev. gén. de Bot.* 24, 1912, p. 177.

(32) SIGMUND, W. Ueber die Einwirkung chemischer Agentzien auf die Keimung. *Landw. Versuchs-St.* 47, 1896, p. 1.

(33) SPRENGEL, C. *Meine Erfahrungen im Gebiete der allgemeinen und speziellen Pflanzenkultur*, Bd. 1, Leipzig, 1847, p. 86.

(34) TOWNSEND, C. O. The Effect of Hydrocyanic Acid Gas upon the Germination of Seeds. *Proc. Amer. Assoc. Advanc. Sc.* Columbus, 1899, p. 297.

(35) Townsend, C. O. The Effect of Hydrocyanic Acid Gas upon Grains and Other Seeds. *Bot. Gaz.* 31, 1901, p. 241.

(36) Velten, W. Ueber die Folgen der Einwirkung der Temperatur auf die Keimfähigkeit und Keimkraft des Samen von *Pinus Picea* Du Roi. *Sitzungsber. d. Kais. Akad. d. Wiss. math.-naturwiss. Cl.* Wien, 74, I Abt. 1876, p. 359.

(37) Voelcker, J. A. Woburn Pot-Culture Experiments; The Hills Experiments. *Journ. Roy. Agric. Soc.* England, 61, 1900, p. 553.

(38) —— Woburn Pot-Culture Experiments; The Hills Experiments. *Journ. Roy. Agric. Soc.* England, 62, 1901, p. 317.

(39) —— Woburn Pot-Culture Experiments; The Hills Experiments. *Journ. Roy. Agric. Soc.* England, 64, 1903, p. 348.

(40) —— Woburn Pot-Culture Experiments; The Hills Experiments. *Journ. Roy. Agric. Soc.* England, 73, 1912, p. 314.

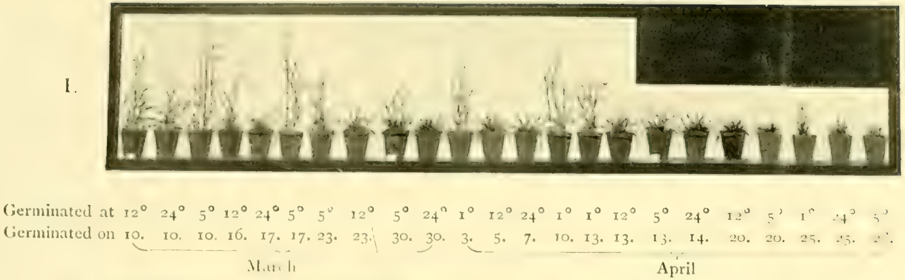
(41) West, C. and Kidd, F. The Controlling Influence of Carbon Dioxide. Part V. On the Production of Primary and Secondary Dormancy in Seeds of *Brassica alba* by means of Boric Acid, and the Relation of Hydrogen-ion Concentration to the Production of Secondary Dormancy. (In the Press.)

(42) Wild, L. J. The Tillering of Wheat. *Journ. of Agric.* (New Zealand), 9, 1914, p. 31.

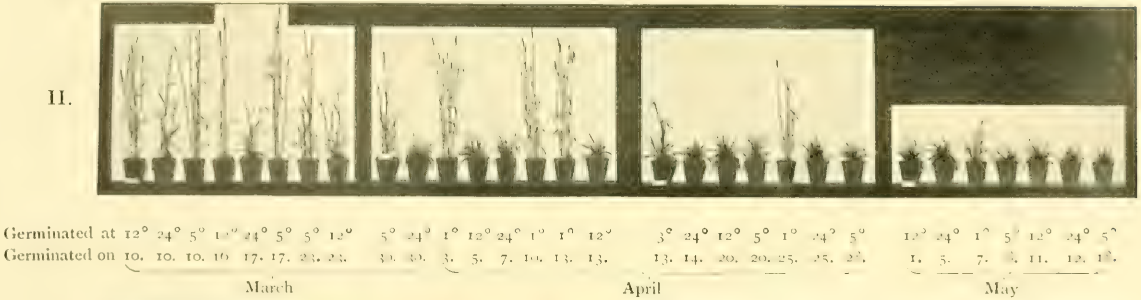
(43) Wollny, E. Das Dörren der Samen. *Oesterr. landw. Wochenblatt*, 5, No. 48, 1879.

(44) —— *Saat und Pflege der landwirtschaftlichen Kulturpflanzen.* Berlin, 1885.

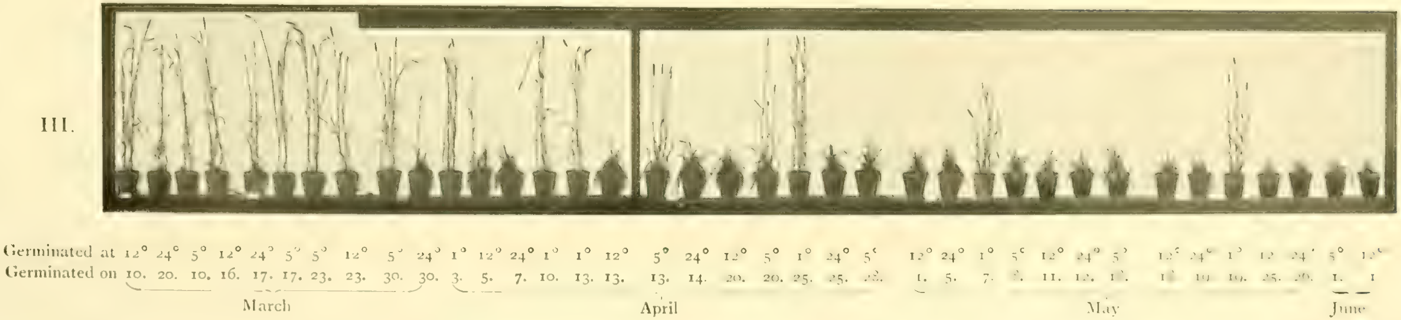
I.


Germinated at 12° 24° 5° 12° 24° 5° 5° 12° 5° 24° 1° 12° 24° 1° 1° 12° 5° 24° 12° 5° 1° 24° 5°
Germinated on 10. 10. 10. 16. 17. 17. 23. 23. 30. 30. 3. 5. 7. 10. 13. 13. 13. 14. 20. 20. 25. 25. 28.
March
April

II.


Germinated at 12° 24° 5° 12° 24° 5° 5° 12° 5° 24° 1° 12° 24° 1° 1° 12° 5° 24° 12° 5° 1° 24° 5° 12° 24° 1° 5° 12° 24° 5°
Germinated on 10. 10. 10. 16. 17. 17. 23. 23. 30. 30. 3. 5. 7. 10. 13. 13. 13. 14. 20. 20. 25. 25. 28. 1. 5. 7. 8. 11. 12. 18.
March
April
May

III.


Germinated at 12° 24° 5° 12° 24° 5° 5° 12° 5° 24° 1° 12° 24° 1° 1° 12° 5° 24° 12° 5° 1° 24° 5° 12° 24° 1° 5° 12° 24° 5° 12° 24° 1° 12° 24° 5° 12°
Germinated on 10. 20. 10. 16. 17. 17. 23. 23. 30. 30. 3. 5. 7. 10. 13. 13. 13. 14. 20. 20. 25. 25. 28. 1. 5. 7. 8. 11. 12. 18. 18. 19. 19. 25. 29. 1. 1
March
April
May
June

The development of "Petkuser" Winter Rye in relation to the germination temperature and the time of germination (after Gassner).

Fig. I was photographed on June 8th. Fig. II was photographed on June 27th. Fig. III was photographed on July 26th.

STUDIES IN BACTERIOSIS. III.

A BACTERIAL LEAF-SPOT DISEASE OF *PROTEA CYNAROIDES*, EXHIBITING A HOST REACTION OF POSSIBLY BACTERIOLYTIC NATURE.

By SYDNEY G. PAINE and H. STANSFIELD.

(*From the Department of Plant Physiology and Pathology, Imperial College of Science and Technology, London.*)

(With Plate II.)

The disease was observed on plants of *Protea cynaroides* in the houses at Kew Gardens where, for a number of years—practically since the introduction of this species to the Gardens—it has caused considerable disfigurement to the plants. It occurs on the leaves of all the older plants and shows itself on the leaves of seedlings when these have reached a height of some 10 or 12 inches.

SYMPTOMS OF THE DISEASE.

The disease is characterised by numerous dome-shaped blisters of a reddish-brown colour scattered promiscuously over the lamina of the leaf, mainly, though not entirely, upon the upper surface. They vary in diameter from one to three millimetres and the surface of the blisters is raised half to one millimetre above the general level of the leaf. On the younger leaves in place of the brown blisters there occur rather wider areas whose surface is frequently depressed by shrinkage of the underlying cells. These areas have a diameter up to five or six millimetres, and still larger patches arise through the coalescence of several such spots. The colour of these depressed areas is much brighter than that of the blister-like spots and is either a uniform red or a reddish-brown surrounded by a zone of bright vermilion. The vermilion colour is very conspicuous when the leaf is held up to the light. On examination in this way by transmitted light every spot exhibits a clear translucent halo in a zone of one or two millimetres round the spot. The appearance of the diseased tissue and the nature of the cell contents are identical in the raised and depressed areas; and, as will be described later, an organism has been isolated from the dead tissue of one type of spot which on inoculation into a healthy leaf has given rise to a spot of the other type; there is therefore no doubt that both types of spot have a common origin. It is not known whether the one changes into the other, or whether they are the result of difference in age of the leaf at the time infection took place. Spots of both types occur on one and the same leaf and may be recognised in the photograph (Fig. 1 *A*); the sunken type with bright red colour (Fig. 1 *B*) is, however, the only one which has resulted from artificial infection of young seedling plants (Fig. 2). For these figures see Plate II.

PATHOLOGICAL ANATOMY.

Microscopical examination of a section through one of the spots shows the cells completely disorganised, the normal contents having given place to a yellow or brown gum-like mass. In fresh material the mass completely fills the cavity of the cell, but in fixed material it is found to have contracted slightly from the walls of the cells (Figs. 4 and 5). The group of affected cells is frequently cut off from the surrounding tissue by a zone of three or four layers of cork cells. No fungal mycelium is present in the diseased tissue, and no bacteria can be found in the intercellular spaces. In many spots clear evidence of the parasitic origin of the disease is lacking, but in others one or two cells, usually epidermal cells, are found filled with granules which have all the appearance of micrococci and which take the bacterial stains strongly (Fig. 3). In these cells the gum-like substance is either absent altogether or is present in such small quantity that only a very faint yellow colour is observable. In the majority of the diseased cells, however, this substance is present, and exhibits a variety of differences in its minute structure and staining capacity which are thought to have considerable significance. An attempt to reproduce these differences by shading has been made in Figs. 4 and 5; the drawings are from a hand section through a "blister-spot," and the section was stained with carbol fuchsin and partially decolourised with 50 per cent. alcohol[1].

The substance in some cells retains the fuchsin strongly and includes a mass of closely compacted granules which stain still more strongly with fuchsin and other bacterial stains. Fig. 5 shows several such masses.

---

[1] The similarity in actinic value of the red and orange rays makes it impossible to demonstrate these differences of colour and structure by a photographic process.

In the cell marked *A* the gummy mass was densely stained and appeared very definitely granular, the substance surrounding the granular mass possessed a fine foam-structure. In cell *B* granules of about the size of small bacteria could be distinctly recognised; here also the matrix showed a foam-structure, but of a coarser character than in cell *A*. In cell *C* masses of densely staining material were surrounded by a mass of gum which had become very vacuolate and which took up the fuchsin stain only weakly. Cell *D* was almost completely filled with similar vacuolate material. The cells which are shaded uniformly in Figs. 4 and 5 were filled entirely with structureless transparent gum-like material which showed different degrees of staining capacity in the different cells, as is shown, for instance, in the cells marked *A* and *B*, Fig. 4. The substance in cell *A* was entirely unstained by fuchsin and possessed a

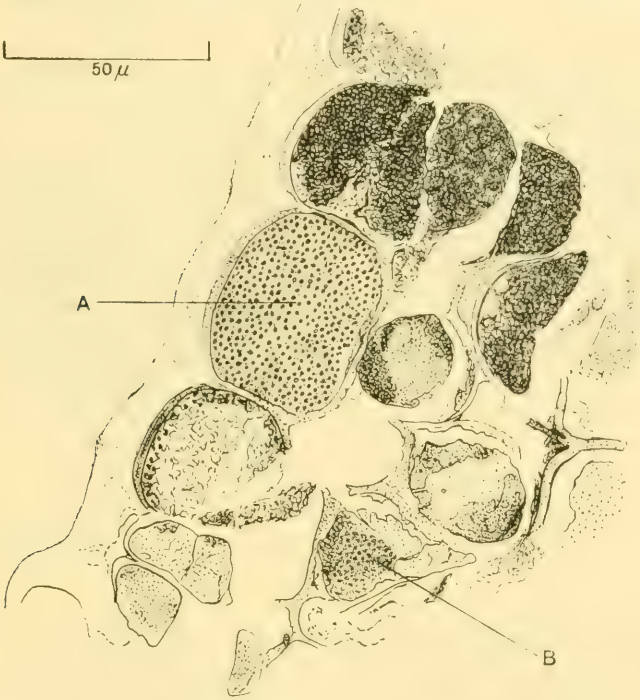


Fig. 3. Drawn with the aid of the camera lucida from a microtome section 4μ in thickness through a leaf spot of *Protea cynaroides*; note the very frangible nature of the gum-like substance filling the majority of the cells. *A*, cell filled with granules believed to be bacteria, the cause of the disease; *B*, cell filled with gum in which are embedded similar granules which appear to be in process of dissolution.

clear bright amber colour, while in cell *B* it retained a fairly strong fuchsin stain. We have, then, what appears to be a series of stages in the disappearance of such granules as are represented in Fig. 3. The nature of these granules is not definitely established, but a micro-organism has been isolated from diseased tissue with which these bodies compare closely in size, and since bacteria in the diseased tissue are indicated in no other way and, moreover, the granules stain deeply with carbol fuchsin and Victoria blue, the assumption of their bacterial nature seems amply justified. It is not always possible to demonstrate in sections of diseased tissue such bacteria-like granules, but in all cases masses of the granular gummy substance occur in various degrees of granulation and of staining capacity, and the degree of granulation always runs *pari passu* with the power of retention of a bacterial stain. One is therefore led to assume that bacteria entering the cell are early

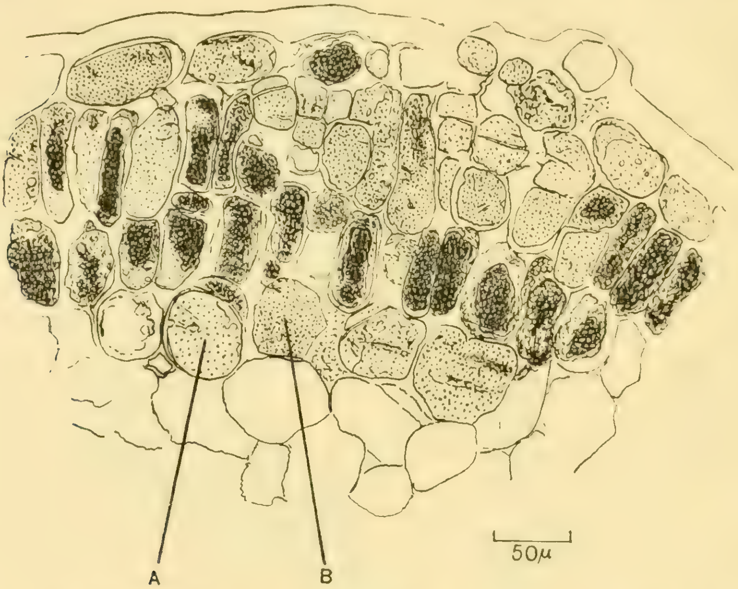


Fig. 4. Drawn with the aid of the camera lucida from a hand section through a "blister-spot" on the leaf of *Protea cynaroides.* The cells shaded darkly contain a more or less granular matter embedded in a gum-like matrix, and they retain a fuchsin stain in proportion to the degree of granulation. The cells shaded uniformly contain structureless transparent masses of gum which reacted variously with fuchsin, some, as cell *A*, lost all the stain and possessed a clear amber colour after treatment of the section with 50 per cent. alcohol, while neighbouring cells, as cell *B*, retained a fairly strong fuchsin stain.

killed by some poisonous substance and eventually disappear by a process of solution, the vacuolation of the gum being interpreted as marking

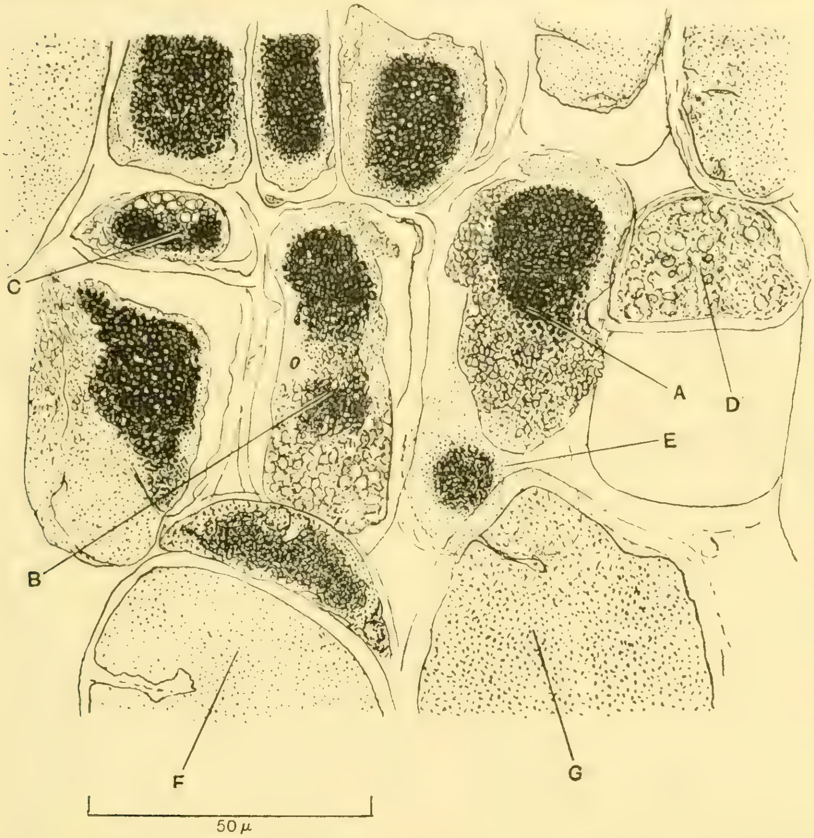


Fig. 5. Portion of the section shown in Fig. 4, more highly magnified. *A*, cell containing a gum-like matrix with foamy structure and including a densely granular and deeply stained mass believed to represent bacteria in process of solution, the foamy nature of the matrix may possibly mark the presence of degradation products from similar granules. *B*, cell containing similar contents, the more open nature of the foam indicates perhaps a later stage in the process of degradation. *C*, cell containing what appear to be oily drops in the gum-like matrix. *D*, cell containing vacuolate gum in which bacteria-like granules can no longer be recognised. *E*, a cell similar to that marked *A*, but out of focus. *F*, cell *A* of Fig. 4, containing perfectly structureless amber coloured gum. *G*, cell *B* of Fig. 4, containing similar transparent gum but stained fairly strongly with fuchsin, a feature which is taken to indicate that some bacterial substance is still present in the gum.

the presence of certain degradation products of the bacterial cell. (There may possibly be an analogy here with the solution of a bacillus, as for example of the cholera bacillus, in the bacteriolytic serum of an immunised animal.) This view is supported by the fact that in sections of some of the spots bacteria cannot be definitely recognised, and further by the fact that when attempts are made to isolate the parasite many of the spots appear to be sterile. A somewhat similar pathological condition has been described by Potter[1] in a brief account of a raised leaf-spot disease of an orchid, *Odontoglossum Uro-Skinneri*; the swelling of the tissue is there attributed to the production of a mucilaginous substance in which bacteria, believed to be the cause of the disease, are found embedded. It is possible that the substance is of the same nature in both cases, but in *Odontoglossum* it is described and figured as occupying the intercellular spaces while in *Protea* it is found only within the cells.

Some attempt was made to determine the nature of this substance in *Protea*, but unfortunately the amount of material available was too limited to permit of any extensive investigation of the part it plays in the bacteriolytic process or of its chemical composition. First it should be noted that the presence of this substance is not confined solely to the diseased areas, but appears in its structureless non-staining variety wherever the tissues are wounded and also in certain cells in the neighbourhood of the vascular bundles. It may perhaps be an ordinary tannin product of the host cells and, if the assumption of bacteriolysis is correct, may serve in the diseased area simply as a vehicle in which the solution of bacteria is brought about by some other agency, possibly by autolysis.

The gummy substance becomes very brittle in fixed material, and in consequence it has been found very difficult to prepare good sections of the diseased tissue, and almost impossible to obtain microtome sections. The irregularities and the fissures in the substance depicted in Figs. 3 and 5 give some idea of its mechanical texture; the material from which the sections here shown were prepared had been preserved in weak formalin.

Fig. 3 was drawn from a very imperfect microtome section typical of several attempts to cut the material on the microtome; with the exception of one of the epidermal cells only fragments of the tissue were obtained in spite of the fact that the cuticle, itself a difficult subject for the knife, was cut perfectly. The epidermal cell referred to, presumably recently invaded by bacteria, possessed a matrix of a scarcely perceptible yellow tinge, while the contents of many of the neighbouring cells were deep yellow to dark amber in shade[2]. This is taken to indicate that the formation of the gummy substance had only just begun, hence the contents were so little refractory that a tolerable section of this cell was obtained.

---

[1] *Gardeners' Chronicle*, Ser. III, vol. 45, p. 145, 1909.

[2] The bacterial stain employed in this case was Victoria blue, not fuchsin.

In spots on young leaves the yellow material is accompanied by a bright vermilion pigment. This is insoluble in water and in alcohol, even after 24 hours steeping of the tissue in boiling alcohol; it is slightly soluble in ether; it is insoluble in hydrochloric acid but dissolves slowly in cold concentrated sulphuric acid; it is readily soluble in ammonia, from which it is precipitated as a red powder by hydrochloric acid. These reactions, with the exception of sparing solubility in alcohol, are those of phlorotannin red, but solutions of the red precipitate in caustic soda do not show the fluorescence characteristic of this substance (Beilstein, 3rd ed., vol. 2 B, p. 1919). A substance of this character would probably be sufficiently toxic to account for the death of the bacteria; their subsequent disappearance is, however, a matter of pure conjecture.

After extraction of the red pigment by ammonia the yellow substance remains apparently unaltered. It stains black with ferrous sulphate and may perhaps be of the nature of a resino-tannin.

ISOLATION OF THE PARASITE.

The surface of diseased leaves was sterilised by immersion in hydrogen peroxide for one hour, after which the leaves were allowed to dry and the epidermis was removed from a young blister-spot by means of a flamed scalpel. A little of the exposed soft brown tissue was crushed in sterile water and dilution plates in bouillon gelatine and bouillon agar were poured. Several attempts at isolation in this way failed to give any result; this may have been the effect of the treatment with hydrogen peroxide, but it is considered more probable that the organisms in the spots selected had been destroyed in the manner suggested above. Eventually, however, success was attained; numerous colonies appeared on the plates after three days incubation at 20° C. and were apparently all of one type. Repeated platings yielded pure cultures without much difficulty.

INFECTION EXPERIMENTS.

Through the courtesy of the Director of Kew Gardens two small plants of *Protea cynaroides* were available for inoculation. These were sturdy young seedlings six and eight inches in height, and had several young leaves which were quite free from the disease. In all, fourteen experiments were made upon seven separate occasions, using seven different cultures of the organism. The inoculations were made in various ways, and of the fourteen attempts only one failed to produce infection.

Experiment 1. May 29th, 1918. The surface of a leaf of a potted plant was sterilised by washing with alcohol and two inoculations were made by placing a spot of slime from an agar culture (the third transfer from the original isolation) upon the upper surface of the leaf and pricking through this into the leaf with a flamed needle; two controls were made by similarly pricking through slime which had been heated. May 31st: a translucent margin one millimetre wide had appeared round the punctures, and a mucilaginous drop was present above the point of infection; control spots had dried up. June 2nd: tissue was brown in a zone of 2 mm. radius round the prick; control pricks were dry and browned only at the edge of the needle puncture. June 8th: typically diseased spots; controls dried out. Plate cultures from a suspension of the diseased tissue showed on June 10th development of many colonies of two distinct types with a strong preponderance of that characteristic of the disease organism. A second plating from these gave pure cultures which were used in Experiment 3.

Experiment 3. June 12th, 1918. The organism re-isolated from the leaf of Experiment 1 was pricked into a cut leaf placed on moist blotting-paper in a Petri dish and kept at room temperature. June 17th: tissue was brown and typically diseased two millimetres round both infection spots and mucilaginous drops were standing above as in Experiment 1; control pricks had dried up. A suspension of the diseased tissue was employed in Experiment 7.

Experiment 7. June 18th, 1918. Diseased tissue from leaf of Experiment 3 was suspended in sterile water and pricked into a leaf of a growing plant. June 30th: all inoculated spots were typically diseased: all controls had dried up.

Experiment 4. June 14th, 1918. The organism from an agar slope (the fifth transfer from the original) was pricked into a cut leaf with its petiole immersed in sterile water and covered with a bell-jar. It was placed in strong light in the greenhouse laboratory. June 20th: around the two infection pricks the tissue was browned in a spot 4 mm. diameter and this was surrounded by a wider zone 6 or 7 mm. diameter in which the bright vermilion pigment typical of the disease in young leaves had developed abundantly. A photograph of this leaf appears in Plate II, Fig. 2.

Other infections were obtained by hypodermic injection of pure cultures, by placing bacterial slime upon the leaf surface without puncturing the leaf, and by gently rubbing with the finger a water suspension of the organism upon the upper surface of the leaf. Except in one case typical disease resulted from these experiments. Control experiments were made with heated bacterial slime and with a gum arabic solution brought to the opacity of the slime with potato starch. The object of these controls was to determine whether physiological influences, such as the blocking of the stomata or the local shading from light of the tissue, would produce the symptoms of disease. None of these controls showed any browning effect. The brown substance however is formed in response to wounding round the needle pricks in control experiments but, as seen in Plate II, Fig. 2, there is a marked difference in the extent of discolouration between the infection and the control spots.

The fact that infection could be produced by gently rubbing a suspension of the organism over the surface of the leaf would suggest that the mode of entry of the bacteria into the leaf under natural conditions is by way of the stomata. In accordance with the xerophytic habit of the plant the cuticle of the leaf, which is exceedingly thick, is raised above the guard cells of the stoma in the form of a spacious cup (Fig. 4) eminently suited to catch water and act as a port of entry for bacteria to the chamber below. The spots always appear to have developed in connection with the stomata, and in a large number of cases a single stoma has been found occupying the very centre of the surface of the diseased area, though no sections of diseased spots have revealed the presence of bacteria in either the stoma itself or in the sub-stomatal chamber.

DESCRIPTION OF THE CAUSAL ORGANISM.

(i) *Morphological Characters.*

Form and Size. The organism taken from an agar slope incubated for 24 hours at 22° C. is a small oval rod $0{\cdot}8\text{–}1{\cdot}6\mu \times 0{\cdot}6\text{–}0{\cdot}8\mu$; pairs up to $2{\cdot}5\mu \times 0{\cdot}8\mu$. In sections of diseased spots where organisms can be found they appear to be of about the same diameter but almost coccoid in form.

Motility. In young cultures the organism is actively motile with a free swimming motion. The flagella stain quite readily by the method of van Ermengen and a beautiful preparation was obtained by the method of Plimmer as yet unpublished[1]; they are from one to three in number, 10–20μ in length and are unipolar (Fig. 6). The organism is therefore a *Pseudomonas*. Motility soon ceases in cultures on solid media, even after 24 hours at 22° C. only a few individuals are found in motion; in liquefied gelatine and in bouillon, however, motility was observed in cultures of three days incubation at the above temperature.

---

[1] It is hoped that the publication of this method will not be long delayed.

Staining. Positive results were obtained with the usual bacterial stains and with Gram's stain, negative results with spore stains and capsule stains.

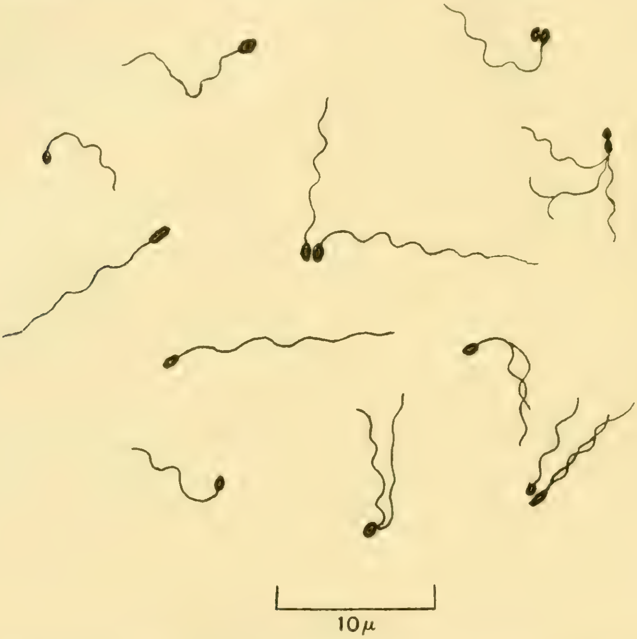


Fig. 6. Drawn with the aid of the camera lucida from a preparation of *Pseudomonas Proteamaculans* stained by the method of Plimmer (unpublished).

(ii) *Cultural Characters.*

The organism grows luxuriantly on solid media of various composition and of varying H ion concentration up to about + 30 of Fuller's Scale.

Gelatine streak + 10. Incubated at 22° C. Liquefaction 4 mm. wide and 2 mm. deep after 24 hours; complete liquefaction after 72 hours.

Gelatine stab + 10. Incubated at 22° C. Liquefaction at first crateriform, the crater being 5 mm. wide and 2 mm. deep after 24 hours; later, *i.e.* after 3 days, infundibuliform with a layer of liquid gelatine 6 mm. deep above, the funnel being 7 mm. across at the top and 3 mm. at the bottom.

Agar streak + 10. Incubated at 22° C. Streak from straight wire inoculation 2 to 1 mm. wide after 24 hours, margin entire, surface raised 0·5 mm., "wet shining," dirty white with faint yellow tinge, distinctly yellow when collected on a wire.

Agar stab + 10. Incubated at 22° C. Growth along the stab uniform to bottom with echinate margin, surface growth after 24 hours 3 mm. diameter and raised 0·5 mm.

Potato agar. Incubated at 22° C. Very strong growth after 24 hours. Characters as on bouillon agar but perhaps a trifle more strongly yellow tinted.

Bouillon + 10. Incubated at 22° C. Well clouded after 24 hours. Slight ring but no pellicle.

Thermal Death Point. Twelve tubes of bouillon were placed in a water-bath and raised to 47° C. registered on a thermometer with its bulb immersed in water in a similar tube. The tubes were inoculated in duplicate with a loopful of a bouillon culture of 24 hours growth. The temperature of the bath was raised 2° C. between the inoculation of each pair of tubes and the inoculated tubes were maintained at their appropriate temperatures for 10 minutes, then plunged into cold water. All were incubated at 25° C. for 7 days. The thermal death point was found to lie between 51° and 53° C.

(iii) *Physiological Characters.*

Bouillon ("*Jardox*") + 2 *per cent. sugar.* Acid and gas formed in presence of glucose, sucrose and mannite. The amount of gas was not large and occupied only one-tenth of the volume of a Durham's tube after 7 days incubation at 22° C., and was approximately the same in each case. A slight ring formed, but no pellicle. Bleaching of the litmus occurred at the bottom after 4 days. No acid nor gas formed in lactose bouillon though growth was indicated by slight turbidity and ring formation.

Bouillon ("*Jardox*") + 1 *per cent. nitrate.* Nitrite was present after 24 hours at 22° C. and was still present after 2 months, at which time, by transferring to other media, the organisms were shown to be still viable.

Potato plug. Growth well visible after 24 hours at 22° C., and strongly developed after 48 hours, faint yellow in colour; the surrounding medium was not discoloured. The plug ground in a mortar after 12 days and suspended in 300 c.c. of water gave, when tested with iodine, a more purple colour than a control plug, showing slight diastatic action had occurred.

Uschinsky's solution. No acid and no gas; strong ring and no pellicle.

Litmus milk. Acid after 24 hours at 22° C., loose curd after 2 days, and whey separated after 4 days, whey clear and colourless; curd settled to half the volume of the liquid after 7 days, and still occupied one-third of the volume after 2 months.

NOMENCLATURE.

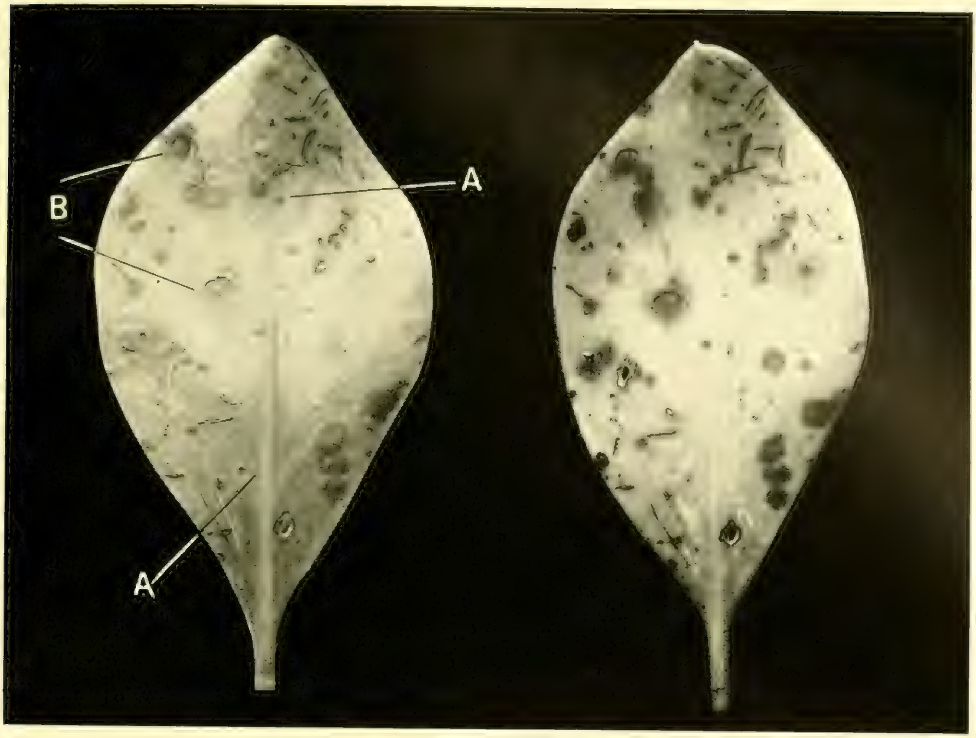
The organism is a pseudomonas and does not agree with any previously described organism. It is therefore believed to be a new species and the name *Pseudomonas Proteamaculans* is suggested for it. According to the system of the American Society of Bacteriologists it is represented by the number 221.1313023.

CONTROL MEASURES.

In the present state of our knowledge the control of bacterial diseases is very difficult. In this instance the bacteria gain entrance to the leaf by way of the stomata and are undoubtedly introduced as a result of syringing the plants. The presence of some antiseptic in the water used for syringing which shall be toxic to the organisms and harmless to the plant therefore suggests itself as a possible means of preventing infection. With this end in view the following experiments were made. Test tubes containing 10 c.c. of the solutions given below were sterilised and inoculated with a loopful from an active culture of *Pseudomonas Proteamaculans*, and after the time stated in each case a loopful was transferred to bouillon agar and plated out. The number of colonies developed at 20° C. was determined after three days incubation.

No.	Solution	Time of exposure	No. of colonies
1	·001 % $HgCl_2$	1 min.	200–300
2	,,	5 ,,	none
3	,,	10 ,,	,,
4	,,	15 ,,	,,
5	$\frac{1}{400}$ formalin	1 ,,	∞
6	,,	5 ,,	100–200
7	,,	10 ,,	none
8	,,	15 ,,	,,
9	·001 % $CuSO_4$	1 ,,	∞
10	,,	5 ,,	∞
11	,,	10 ,,	90
12	,,	15 ,,	40

From this it appears that a solution of mercuric chloride (1 : 10,000) is most efficient, but, in view of the poisonous nature of this substance,

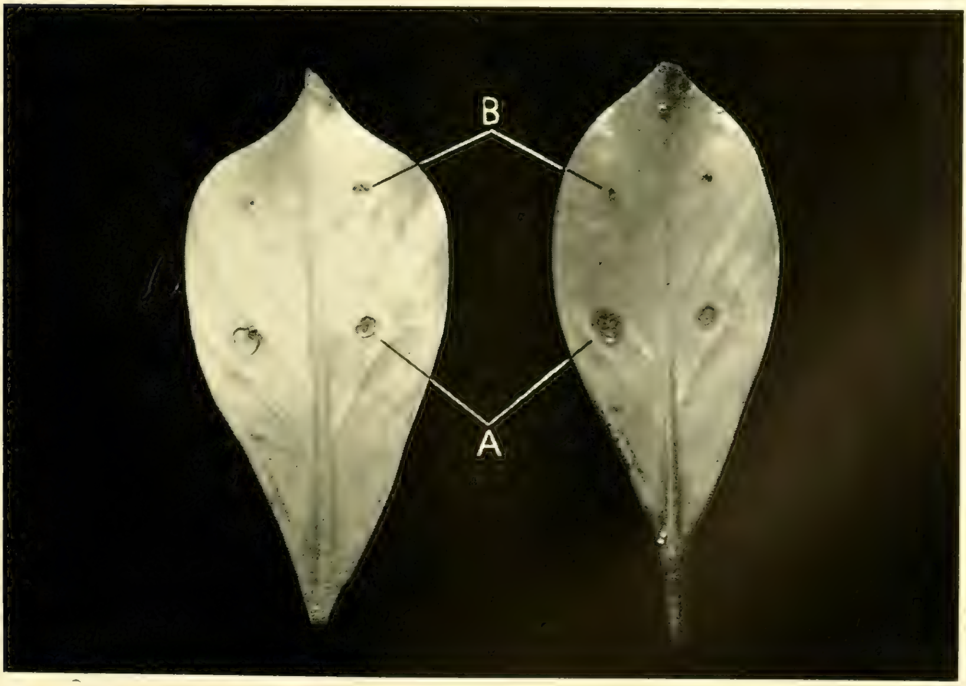


(*a*) (*b*)

Fig. 1.

(*a*) Diseased leaf of *Protea cynaroides* showing two types of bacterial spots, raised blister-like spots at *A* and sunken spots at *B*.

(*b*) The same leaf photographed through an orthochromatic light filter.



(*a*) (*b*)

Fig. 2.

(*a*) Leaf of *Protea cynaroides* artificially infected by means of "prick" inoculations with a pure culture of the causal organism. *A* infection spots; *B* controls.

(*b*) The same leaf photographed through an orthochromatic light filter.

the formalin solution (1 : 400) would be much safer and would probably have the desired effect.

SUMMARY

1. A description is given of a disease of *Protea cynaroides* which is characterised by the development on the leaves of blister-like spots of a brown colour, or of sunken spots of a brown colour with bright vermilion border.

2. The causal organism described is a bacterial parasite for which the name *Pseudomonas Proteamaculans* is suggested.

3. The attacked cells become filled with an amber coloured resin-like substance in which apparently the bacteria become embedded and suffer a process of solution. This solution is either one of autolysis, or there may possibly be an analogy with the bacteriolytic action of the serum of an immunised animal.

4. The vermilion pigment is shown to be closely allied to phloro-tannin red and the resin-like substance is believed to be of the nature of a resino-tannin.

ON THE OCCURRENCE OF THE IMMATURE STAGES OF ANOPHELES IN LONDON.

By FLORENCE E. JARVIS.

The observations recorded below were made between September 1917 and September 1918. The area selected was approximately a circle with its centre at Charing Cross and a radius of about nine miles. The majority of the pieces of water examined were ornamental ponds in the various London parks, but in addition a number of natural ponds, swamps, and ditches were searched.

Positive results for *Anopheles maculipennis* were obtained from sixteen out of a total number of thirty-seven pieces of water investigated. *A. bifurcatus* occurred in one locality; *A. plumbeus* (= *nigripes*) was not observed.

During the spring and early summer of 1918 the presence of immature stages of *A. maculipennis* was noted in or near the outer limit of the selected area only. Later in the season, in August, considerable numbers of larvae were obtained from places much nearer the centre of the circle, *e.g.* Chelsea Physic Garden and Battersea Park. These facts seem to suggest the possible occurrence during the summer of an inward migration of adults from more outlying suburbs. The two places mentioned above lie opposite one another on the north and south sides of the Thames respectively and are enclosed by houses on three sides, the fourth side being open to the river. A migration of adults to Chelsea and Battersea could thus conceivably take place along the course of the river from the marshy districts lying near the mouth. The west and south-west winds however, which prevailed during the greater part of the summer of 1918, would appear to have been able to hinder effectively a migration in this direction. A visit made in September to an ornamental pond in Staple Inn yielded a negative result which could be attributed (1) to the densely-populated nature of the locality, and (2) to the presence of a number of gold-fish in the water.

In the accompanying table are given, in order of date, the pieces of water visited. Many of these proved unsuitable for breeding places, while in certain other cases conditions were apparently favourable but negative results were obtained. Further investigation of these apparently favourable localities is desirable.

Since the presence of larvae of *A. maculipennis* has now been observed as far within the urban district of London as Chelsea, records are needed of the occurrence of adults in this area. Up to the present time adults have only been recorded from suburban localities (Acton, Mitcham, etc.) all lying at a considerable distance from Charing Cross.

In order to make this report as complete as possible, previous records have been incorporated into it. All such records have been drawn from W. D. Lang's *Map showing the known Distribution in England and Wales of the Anopheline Mosquitoes, with explanatory Text and Notes*, published by the British Museum (Natural History), 1918. The Local Government Board's *Reports and Papers on Malaria contracted in England in* 1917 (New Series, no. 119, 1918) has also been consulted, but contains no additional information on the London area.

The writer is extremely indebted to Mr W. D. Lang for his kindness in identifying numerous larvae and adults, to Mr A. J. Grove (Acting Entomological Investigator, Local Government Board), and to Mr Hugh Scott for his assistance throughout the course of the investigations.

TABLE SHOWING PLACES VISITED, IN ORDER OF DATE.

Date	Locality	*A. maculipennis*	*A. bifurcatus*	
28. ix. 1917	Richmond Park	*	—	
2. x. 1917	,, ,,	*	—	
19. x. 1917	Swamp near Southend Pond, Catford, S.E.	—	*	
26. x. 1917	,, ,, ,, ,,	—	*	
30. x. 1917	,, ,, ,, ,,	—	*	
2. xi. 1917	Regent's Park	—	—	
23. xi. 1917	Swamp near Southend Pond	—	*	
27. xi. 1917	Chelsea Physic Garden	—	—	†
28. ii. 1918	Horniman's Museum, Forest Hill, S.E.	—	—	
28. ii. 1918	Dulwich Park, S.E.	—	—	†
1. iii. 1918	Battersea Park	—	—	†
2. iv. 1918	Ruskin Park, Denmark Hill, S.E.	—	—	†
2. iv. 1918	Peckham Rye Park, S.E.	—	—	†
29. iv. 1918	Swamp near Southend Pond	—	*	
29. iv. 1918	White Foot Lane, Hither Green, S.E.	—	—	†
30. iv. 1918	Hayes, Kent	—	—	†
8. v. 1918	Sydenham Wells Park	—	—	†
10. v. 1918	Streatham Common	—	—	†
10. v. 1918	Pond in adjoining field	—	—	†
14. v. 1918	Mitcham Common	*	—	

* denotes the occurrence of eggs, larvae or pupae.

† denotes conditions apparently favourable, though no immature stages found.

TABLE SHOWING PLACES VISITED, IN ORDER OF DATE (*continued*).

Date	Locality	*A. maculipennis*	*A. bifurcatus*	
14. v. 1918	Tooting Bec Common	—	—	
14. v. 1918	Brockwell Park	—	—	
21. v. 1918	Wimbledon Common	—	—	†
21. v. 1918	Putney Heath	—	—	†
28. v. 1918	Ham Common, Richmond	—	—	†
28. v. 1918	Richmond Park	*	—	
31. v. 1918	Bushey Park	*	—	
1. vi. 1918	Regent's Park	—	—	
2. vi. 1918	Chelsea Physic Garden	—	—	†
4. vi. 1918	Swamp near Southend Pond ...	—	—	†
5. vi. 1918	Telegraph Hill Park, New Cross, S.E.	—	—	†
8. vi. 1918	Brent Reservoir, near Hendon ...		—	
11. vi. 1918	Gunnersbury Park	—	—	†
12. vi. 1918	Sydenham Wells Park	—	—	†
15. vi. 1918	Hampstead Extension Fields ...	—	—	
25. vi. 1918	Bloomfield Park, N.W.	—	—	
4. vii. 1918	Finsbury Park	—	—	
8. vii. 1918	Wanstead Park	*	—	
8. vii. 1918	Woodford	*	—	
8. vii. 1918	Higham Park, Epping	—	—	
10. vii. 1918	Ham Common	*	—	
10. vii. 1918	Richmond Park	*	—	
30. vii. 1918	Keston, upper pond	*	—	
1. viii. 1918	Streatham Common	*	—	
1. viii. 1918	Mitcham Common	*	—	
2. viii. 1918	Regent's Park	*	—	
9. viii. 1918	Dulwich Park	—	—	†
9. viii. 1918	Ruskin Park, Denmark Hill, S.E. ...	—	—	†
9. viii. 1918	Peckham Rye Park	*	—	
10. viii. 1918	Telegraph Hill Park	*	—	
15. viii. 1918	Chelsea Physic Garden	*	—	
15. viii. 1918	Battersea Park	*	—	
26. viii. 1918	Putney Heath	*	—	
26. viii. 1918	Wimbledon Common	—	—	†
2. ix. 1918	Hampstead Extension Fields ...	*	—	
2. ix. 1918	Golder's Hill Park	—	—	
2. ix. 1918	Hampstead Ponds	—	—	
2. ix. 1918	Highgate Ponds	—	—	
3. ix. 1918	Wanstead Park	*	—	
7. ix. 1918	Regent's Park	*	—	
9. ix. 1918	Greenwich Park	—	—	†
10. ix. 1918	Swamp near Southend Pond ...	*	*	
11. ix. 1918	Clisson Park, Stoke Newington ...	—	—	
16. ix. 1918	Staple Inn	—	—	

* denotes the occurrence of eggs, larvae or pupae.

† denotes conditions apparently favourable, though no immature stages found.

DETAILED NOTES ON THE FINDING OF IMMATURE STAGES OF *Culicidae*, TOGETHER WITH PREVIOUS RECORDS OF THE OCCURRENCE OF *Anopheles*, IN LONDON.

1. **Anopheles maculipennis**, M.

Keston, upper pond. Large and shallow, with grassy edges except at one end; weed mainly *Elodea*, but not growing very thickly; numerous small fish, aquatic beetles, Gammarids, and pond-skaters. Visited 30. vii. 1918; wind E., hot and dull. Eggs and young larvae numerous.

Peckham Rye Park. Series of small artificial ponds with flowering water-plants and a considerable quantity of green algae. The water is supplied by a tap which is turned on at intervals of a few weeks, or more frequently during dry weather. Grass at edges kept closely cut; at elevation of 100 ft or less. Visited 2. iv. 1918, when no larvae were found. Examined again 9. viii. 1918; wind W. to N.W., warm and sunny; 7 young larvae found; also 2 larvae of *Culex pipiens*.

Telegraph Hill Park, New Cross. Artificial pond with water-lilies, clumps of rushes, and long grass hanging into water from banks. No larvae found on 5. vi. 1918. On 10. viii. 1918, wind N.W., 4 half-grown larvae.

Southend, near Catford. Reedy swamp on the course of the river Ravensbourne, near Southend Pond. Close to main road, at no great distance from houses; becoming partly dried-up in summer; considerable quantity of duckweed; fish present; water clear. Visited 23. xi. 1917, 29. iv. 1918, and 4. vi. 1918, without finding any larvae. On 10. ix. 1918, strong W. wind, with heavy showers at frequent intervals; level of water raised owing to recent heavy rain; one young larva found and pupae, from one of which a male emerged the following day.

Bexley Heath, S.E. of Woolwich. Larvae in clear water of permanent swampy ground with hoof marks, some duckweed, and no fishes; cattle near at hand, also trees; houses within 100 yards; 27. ix. 1917, bright sunshine, temperature 65°; obs. Mrs A. Macdonald (B. Mus. Map, p. 20).

Erith, E. of Woolwich. (1) Larvae in permanent ditches on Picardy Manor Way—swampy ground, where one ditch spreads out after rain and with muddy pools in the course of the other; water clear, but with some weed in both cases; no fishes seen, a few water-scorpions present; houses within 50 yards; road frequented by children; no cattle near. (2) Larvae in shallow part of a permanent ditch in the marsh, with clear water, some *Spirogyra*, no fishes seen; houses within $\frac{1}{4}$ mile; cattle feeding close at hand; no trees; 26. ix. 1917; obs. Mrs A. Macdonald (B. Mus. Map, p. 20).

Battersea Park. At shallow end of the Ladies' Pond, among rushes; 1. iii. 1918, no larvae or pupae found; 15. viii. 1918, wind S.W., hot and sunny, 6 young larvae obtained.

Mitcham Common. Natural pond on golf-course, near L. B. and S. C. Ry; edges very grassy, sloping gradually into water, which contained weed; houses and cattle near, few trees; 14. v. 1918; 5 larvae, very young, with several larvae of *Ochlerotatus dorsalis* and *O. nemorosus* and one larva of *Culex pipiens*; 1. viii. 1918, wind S.E., hot and dull; eggs, larvae and pupae abundant; also all stages of *C. pipiens* swarming.

Putney Heath. Pond very much overgrown with rushes, leading into ditch at each end; at side of main road; cattle and trees near, fishes seen. 21. v. 1918, no larvae found. 26. viii. 1918, wind W., showery, fine at intervals, warm; mature larvae and pupae numerous.

Richmond. (1) *Ham Common.* Broad ditch outside Ham Gate, bordered with rather thickly growing shrubs; water containing a quantity of dead leaves; trees and cattle near, houses at some distance. 28. v. 1918, no stages found. 10. vii. 1918, larvae and pupae numerous.

(2) *Richmond Park.* Three ponds lying close together at a short distance from Ham Gate; two of these were practically similar in character, having the margins somewhat grassy and with short stiff sedge, and containing much *Ranunculus.* The third was very shallow and grassy and when visited on 13. ix. 1918 was almost dry. On 28. ix. 1917, numerous mature and nearly full-grown larvae and several pupae were obtained; on 2. x. 1917, larvae and pupae were rare, but occurred in all three ponds; on 28. v. 1918, 6 young and 2 more developed larvae were obtained from the first two ponds, while none were found in the third; 10. vii. 1918, all stages numerous in the first two ponds and a few in the third; 13. ix. 1918, 3 mature and 4 younger larvae from the first two ponds only.

The Rookery, Streatham Common. Small ornamental ponds with water-lilies and filamentous algae, connected by deeper ditches overhung with shrubs; houses at a considerable distance. On 10. v. 1918, no larvae found. 1. viii. 1918, wind E. to S.E., hot and cloudy; from one of the deeper ditches were obtained 4 young larvae; the water had been changed about two weeks previous to examination and was partly covered with duckweed.

Bushey Park. In broad stream connected with two ponds lying on the Hampton side of the Diana Fountain; edges with coarse grass, forgetme-not, brook-lime; tadpoles and dragonfly nymphs and pupae abundant. 31. v. 1918, wind S.E., hot and sunny; 2 mature larvae found.

Chelsea Physic Garden. Several artificial ponds with algae, *Elodea*, water-lilies or rushes; 27. xi. 1917 and 2. vi. 1918, no larvae found; 15. viii. 1918, in one pond with many rushes were found 8 larvae (imagines reared).

Hampstead Extension Fields. Muddy swamp, overgrown with reeds, enlarging at one end into a shallow pond with filamentous algae and flowering plants; trees near, houses at no great distance. 15. vi. 1918, no larvae found. 2. ix. 1918, from pond were taken two larvae and one pupa, also *C. pipiens*; from swamp, *Culex pipiens* and 2 larvae of *Ochlerotatus nemorosus*.

Regent's Park. Artificial stream in the grounds of Bedford College. Stream arranged in a series of terraces; water had not been turned on for some months, but rain had collected to varying depths; water contained fallen leaves, while long grass hung in from edges. 22. xi. 1917 and 1. vi. 1918, no larvae found. 2. viii. 1918, water at a depth of about six inches, wind S.E. to S.; numerous larvae, mostly well-developed, a few young forms; swarms of larvae and pupae of *C. pipiens* present. 7. ix. 1918, 4 young larvae, also *C. pipiens*, though less abundant than in August.

Wanstead Park. Three large ponds, *A*, *B*, and *C*. *A*, nearest the main road, is shallow, with clumps of rushes at either end, banks not grassy; *B* has concrete edges, no plants, and is used for boating; while *C* is shallow, especially at one end where there are water-plants, and is surrounded by trees. 8. vii. 1918, numerous larvae among the rushes in *A*; 3. ix. 1918, 2 full-grown larvae from shallow end of *C*.

Woodford. Small pond at the side of the main road immediately beyond the termination of the electric tramway. Water dirty, containing much weed, mainly *Ranunculus*, debris, filamentous algae and dead leaves. 8. vii. 1918, eggs, larvae and pupae abundant; a second larger pond, further from the road, deeper and with less weed, yielded a few larvae.

London, Albert Dock. Larvae, 1901 (B. Mus. Map, p. 14).

2. **Anopheles bifurcatus**, L.

Southend, Catford. Swamp on the course of the river Ravensbourne (see under *A. maculipennis*). 23. xi. 1917, 19. ix. 1917 and 26. ix. 1917, numerous larvae found, also larvae of *Theobaldia morsitans*; 29. iv. 1918, 2 mature larvae and several pupae; 4. vi. 1918, larvae and pupae of

Culex pipiens only; 10. ix. 1918, 2 half-grown larvae, also *A. maculipennis.*

Richmond. (1) At 50–100 ft (*a*) a few larvae in one (middle) pond of Pen Ponds in Richmond Park; absent in upper pond, though conditions are similar; margins grassy; short rushes; (*b*) larvae fairly numerous in a similar pond in park near Ham Gate; (*c*) many pupae and a few larvae in a little grass-bordered stream near Roehampton Gate. Obs. L. Cobbett, 18. x. 1900 (B. Mus. Map, p. 46).

3. **Anopheles plumbeus,** Steph.

Epping Forest. In root-holes in trees. Obs. A. Bacot (B. Mus. Map, p. 49).

4. **Anopheles** sp.

Mitcham Common. (1) 5 larvae, with *Corethra* and *Chironomus* larvae, in sedgy pool behind monument on road between Mitcham and Croydon, 26. ix. 1917; det. Prof. H. M. Lefroy. (2) 8 larvae from next pool in same place, x. 1917; subsequent weekly visits all through x. and xi. failed to produce any larvae. Obs. Miss L. E. Cheesman (B. Mus. Map, p. 57).

Wimbledon Common. 3 larvae in a ditch bordering the high road, 15. ix. 1917; obs. Miss L. E. Cheesman (B. Mus. Map, p. 57).

5. **Culex pipiens,** L.

Golder's Hill Park	2. ix. 1918	
Mitcham Common	26. viii. 1918	Swarms of eggs, larvae, and pupae, with those of *A. maculipennis*
Peckham Rye Park	9. viii. 1918	Two larvae, with larvae of *A. maculipennis*
Regent's Park	2. viii. 1918	Eggs, larvae and pupae abundant, with larvae of *A. maculipennis*
Richmond	28. v. 1918	A few larvae in pond near Ham Gate
Southend, Catford	4. vi. 1918	Larvae and pupae
Streatham Common, in field adjoining the Rookery	1. viii. 1918	
Sydenham Wells Park	12. vi. 1918	One pupa
Wimbledon Common	26. viii. 1918	A few larvae and pupae in pond near main road; larvae and pupae in pond near windmill

6. **Theobaldia morsitans,** Theo.

Southend, Catford	19. x. 1917–23. xi. 1917	Larvae numerous, with those of *A. bifurcatus*
White Foot Lane, Hither Green	29. iv. 1918	One larva, with larva of *O. dorsalis*

7. **Ochlerotatus dorsalis,** Mg.

Mitcham Common	14. v. 1918	Larvae and pupae numerous, with larvae of *A. maculipennis* and *O. nemorosus*
White Foot Lane, Hither Green	29. iv. 1918	One larva, with larva of *Th. morsitans*
Wimbledon Common	21. v. 1918	Two larvae in ditch near main road

8. **Ochlerotatus nemorosus.**

Hampstead Extension Fields ...	2. ix. 1918	Two larvae in reedy swamp
Mitcham Common	14. v. 1918	Larvae and pupae, with larvae of *A. maculipennis* and *O. dorsalis*
Wimbledon Common	21. v. 1918	Several pupae in ditch, with larvae of *O. dorsalis*

IMPERIAL COLLEGE OF SCIENCE,
LONDON.

THE DISTRIBUTION OF PARASITE-INFECTED FISH.

By H. CHAS. WILLIAMSON, M.A., D.Sc.

(*Fishery Board for Scotland, Aberdeen.*)

Among the fish landed at Aberdeen there are two notable classes that are infected by parasites, and it appears that they can be traced to two definite areas of the sea. I refer to what are known as "spotted haddocks," and "worm-infested codlings."

The spotted haddock is a fish of plump condition, in the muscles of which are distributed the cysts of a peculiar parasite which has been named *Dokus adus* Fig. 1, *pa*. A somewhat similar organism was found by Hofer in diseased trout. The infected trout became lethargic and swam about intermittently in a staggering fashion. Hofer regarded the parasite as a sporozoan. Pleyn and Mulsow however found a fungoid-like budding in cultures of the cysts, and they came to the conclusion that it was a fungus. They named it *Ichthyophonus hoferi*. The parasite was

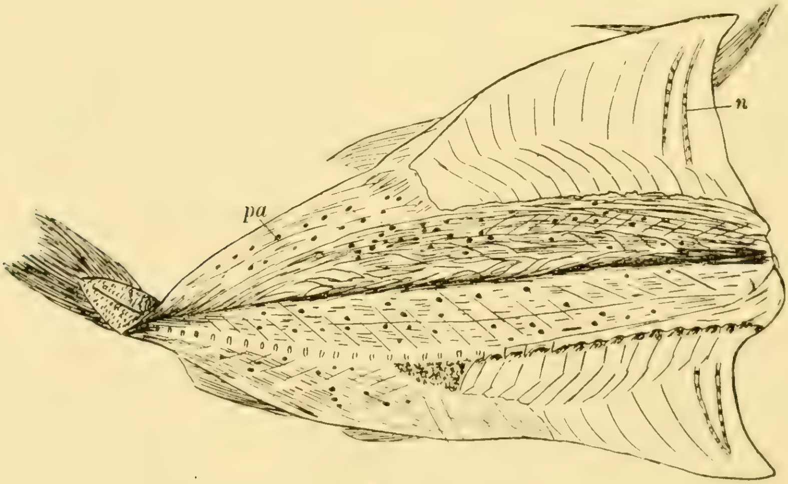


Fig. 1.

found in the liver, kidney, heart, muscles, and sometimes the brain of the trout. The staggering movements were not however always present.

Johnstone has described a fungus, apparently nearly related to the preceding; it occurred in plaice kept in the hatchery pond on the Isle of Man. Infected fish swam about languidly, but showed neither evidence of giddiness, nor lack of co-ordination in their movements.

Externally the spotted haddock is often firm and hard: but when it is split for curing, the flesh emits an unpleasant smell, which is to some extent reminiscent of creasote. The smell may not be noticed in the fresh condition, but it becomes evident after the fish has been smoked. If the cured fish are kept hanging a day after smoking, before they are packed, the odour seems to be accentuated. The smell may be detected in the smoke kiln. Such fish are said to have a sour taste: the flesh when smoked has sometimes a greenish tint and, when observed, they are rejected.

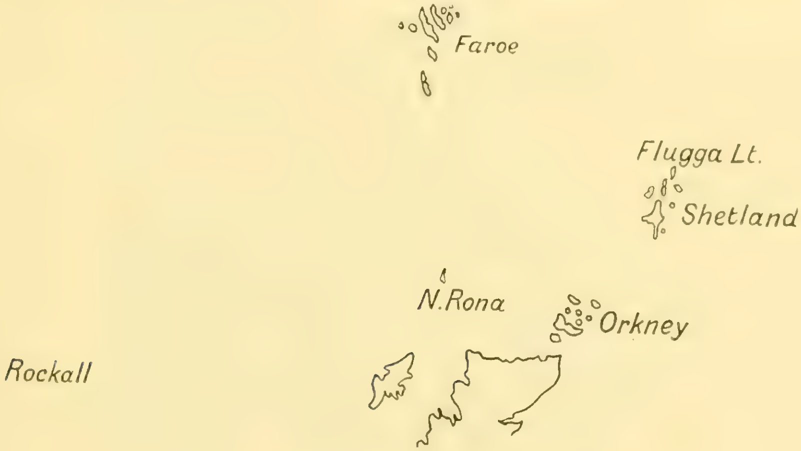


Fig. 2.

The main weight of the evidence at present available points to the conclusion that the spotted haddocks are not found among the North Sea fish landed at Aberdeen, although in the opinion of some observers they are so. There is however general agreement that they occur frequently among the haddocks caught at Shetland, both line- and trawl-caught. The West of Orkney also is given as a locality of origin. Difference of opinion exists as to whether they come from the West of Scotland. Infected fish, both large and small, are found all the year round, but more commonly in warm weather.

These haddocks are generally also infected with trematode cysts in the anterior spinal nerves which are visible on the inside surface of the abdomen (*n*. Fig. 1). Some of the haddocks caught near Aberdeen have these trematode parasites, an infection which is recorded by Lebour as common.

The spotted haddock is not known to occur in either the Iceland or Faroe fisheries. The Faroe haddock appears to be on the whole richer in flesh than the Shetland or North Sea fish, and it does not lose condition after spawning, so much, or for so long a period as the fish from the two other regions.

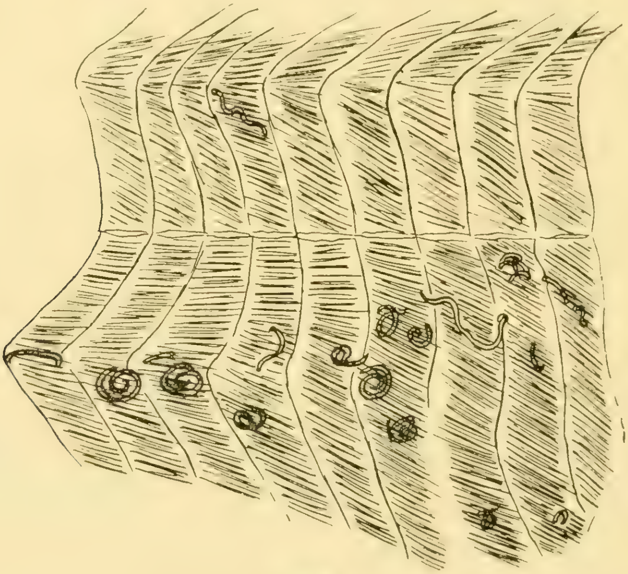


Fig. 3.

The spotted haddock was, I am informed, unknown in Aberdeen seventeen years ago, and one gentleman who cured haddocks on the west coast of Shetland (Walls, Scalloway) twenty-five years ago did not know them. It is said however, that defective haddocks, possibly spotted, had been sometimes taken twenty-five years ago in June in nets which had sunk to the bottom with weight of herrings, between Ve Skerries and Blue Mull Sound.

The affected codlings exhibit coiled nematodes scattered singly through the muscles: they are taken at Faroe, Rona and Rockall: especially in the first-mentioned fishing region. At present it is believed they do not occur among North Sea fish. The infection at Faroe appears to be seasonal, *e.g.* in summer.

Fig. 3 exhibits a portion of the flesh of an infected codling. It was obtained from an Aberdeen fish-yard. The place of origin of the fish was not ascertained. Fig. 4 shows a matted group of nematodes (*N*) inside the abdominal cavity of the same fish: the worms are attached to the peritoneum (*pt*).

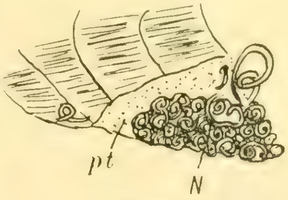


Fig. 4.

The nematodes do not seem to injure the muscle: they are immature and may be about one inch in length. They resemble in some respects larval stages of *Ascaris decipiens* described by Linstow. Larval and adult specimens of this worm were found in profusion in the alimentary tract of two species of seal.

The muscle worm is a very resistant form: it survives the preparation of the fish into the smoked fillet. During that process it is in brine pickle for half-an-hour, and afterwards smoked for from three-quarters of an hour to two hours. A fillet prepared in this way was kept for thirteen days: at the end of the period it smelled offensively. Live worms were dissected out at intervals from the first to the thirteenth day. In a second case the fillet was exposed to the brine and smoke for double the usual time. Thereafter two of four nematodes which were extracted were found to be alive. Nine days later a number of worms were taken out, but all were apparently dead. In a third experiment the cod fillet was dried in the open air: no salt was used. Three months later the fish was very hard. When some of the worms from it were put into sea water they swelled up and became plump. A little movement was detected in one or two cases, but there was no clear evidence that any individual was actually alive.

The worm-infection of the muscle is not restricted to the codling: it occurs in tusk, saith, and I believe also in haddock. The distribution of the affected members of these species is less clear.

It is interesting to note that the spotted haddock occurs at Shetland, but is absent from Faroe; the worm-infected codling exhibits the reverse distribution. A locality or environment may thus have a favourable or unfavourable selective influence on its fish population. The two regions form the margins of the 150 miles wide channel through which the warmer and salter Atlantic current pours into the Norwegian Sea. Trawling is limited on each side to a zone approximately 30 miles broad: the channel has towards its middle a depth of over 600 fathoms. The deepest part of the channel is stated by Helland-Hansen to be covered nearly always with water of a temperature below 32° F. This water is an offshoot from the bottom water of the Norwegian Sea. It has been found that the bottom water runs nearer to the surface in the southern than in the northern part. The depth of the Atlantic current may be from 2 to 300 fathoms. Owing to the influence of the earth's rotation it is, according to Petersson, bent to the east and it sends a branch round Orkney and Shetland over the northern North Sea plateau into the depths of the Norwegian channel as far as to the Skager Rak. The trawl fishery is carried on in this water of Atlantic origin over the whole northern North Sea plateau (deeper than 43 fathoms), as far as the Dogger Bank, and over the western and southern slope of the Norwegian channel (Great Fisher Bank, Jutland Bank, etc.).

Whether the Atlantic current has any special influence with regard to the parasite-infection of the fish is an obscure question, as is also the question whether the fish caught at Shetland for example have been born in some other region. Schmidt deals with the distribution of the fry of the cod, haddock, etc. He says that the pelagic fry (*i.e.* the early stages which have not yet taken up life on the bottom) of the cod produced on the coastal banks at Iceland cannot be carried away from that island to other coasts by currents. It is said however that Iceland cod occur among the fish caught at Faroe and landed at Aberdeen. It would appear also that the fry do not leave the Faroe region to any important extent, with the exception perhaps of some migration from the banks south of the islands. The North and Norwegian Seas receive from the Atlantic a large import of haddock, ling, etc. in the pelagic stage.

Until more extended investigations are made, it may be tentatively concluded that the infected haddocks and cod are restricted in their distribution, and one would be inclined therefore to look for the cause in the local environmental factors, but the problem is a very wide and intricate one.

OBSERVATIONS ON THE HABITS OF CERTAIN FLIES, ESPECIALLY OF THOSE BREEDING IN MANURE.

By J. E. M. MELLOR, B.A.

(With 6 figures and 4 Charts.)

CONTENTS.

Preface:

PAGE
Discussion of best method and time of attacking the fly problem 53
Summary of Views of Writers on Hibernation of *M. domestica* up to 1916 54
Outline of work undertaken 61

Winter observations:

Places searched for larvae and pupae; Similar observations by other observers; Methods; Parasites; Summary . 62
List of flies bred from larvae and pupae collected during Winter 64

Distribution of Flies during Summer and Autumn:

Places visited: Note on feeding habits of *Stomoxys* . . 66

Observations on Horse Manure Heaps, in Summer:

Outline of Experiments; Method; Summary of observations on temperature; emergence of flies; Lack of attraction of fermented manure for adults and lack of nutriment for larvae of *M. domestica* 68
Use of Creosote Oil Mixture on Manure to prevent Fly development 74

Burial of Material infested by Fly Larvae:

Military Manual of Elementary Hygiene; Previous observations—Henri Fabre, Graham-Smith; Methods employed; Results; Table showing flies emerged; Table showing height to which larvae climbed before pupating 80
Summary 85
References 87
Charts of Temperature Curves obtained in Manure Experiments (pp. 72, 73, 76, 77)

PREFACE.

SINCE the relation of flies to certain diseases—and the possibility of that relation being of importance—was first appreciated, much attention has been directed to their control, and their habits and life histories have been widely studied. The problem of fly-control may be dealt with by three methods: (1) destruction of the adult; (2) destruction of the immature stages; (3) perfect and thorough sanitation.

Flies are a corollary of insanitary conditions. "No dirt, no flies." In those parts of modern cities, in which strict sanitation is observed, flies are, probably, not of great importance; but little hope can be entertained of freeing the poorer parts of our own towns and cities, much less those of Eastern countries, from the danger of their presence until legislation and education are much improved.

Method 3, therefore, entails, not only legislation but the alteration, in many cases, of ancient habits, and so is not likely to be applied immediately, still less universally. Method 1, as will be shown later, can never be either thorough or permanent.

Under these circumstances the importance of adopting the second method cannot be too strongly advocated. There are, however, occasions when circumstances necessitate the use of the first method; for instance, when either it is not possible to obtain authority to control the breeding places; or they are too large to be dealt with by the means at hand.

Since the house-fly (*Musca domestica*) has such a wide geographical distribution, it is probable that its life history is variously modified in different parts of the world. This modification will probably depend on climatic conditions—especially those of sunshine and temperature—and the presence or absence of insect and fungoid enemies. Portchinsky (1913) writes that in July 1911 he found very large numbers of *M. domestica* in and about the houses and stables of newly founded farms, on the dry arid steppes, in the southern part of the Government of Stavropol (N. Caucasus); that there were no *Hydrotaea*, *Myospila meditabunda*, or *Polyetes albolineata*, and that *Muscina stabulans* was rarely found on these farms; and that in the open country away from the houses *M. domestica* flourished in enormous numbers in the total absence of their chief enemies.

In England and countries with a similar climate, the year may be divided into two seasons as regards fly control—namely, May to the beginning of November and from November to May (Graham-Smith (1916) chart 4)[1]. In summer it seems hopeless to attempt to deal thoroughly with the fly pest by method 1—destruction of the adult. Howard's figures (1912) give an unnecessarily alarming idea of the number of descendants from a single pair of flies. Graham-Smith (1916) showed that the descendants of each female blowfly during the season numbered 130 individuals instead of 1012 millions.

---

[1] This refers to flies generally. As regards *Musca domestica* the period during which the adults are most numerous lasts from July to October. The remainder of the year presents the weakest part of the life-history of the house-fly. If breeding places were rigorously attacked particularly at this season, the numbers emerging between June and October would be greatly diminished.

In Howard's calculations no account was taken of natural dangers, such as lack of food, the ravages of carnivorous larvae, hymenopterous parasites and inclement weather.

On the other hand, the escape of but a few females may be sufficient to ensure the continuance of the multitudes of flies. Moreover, owing to the extremely short preoviposition[1] period, the chance of killing the majority of females before they oviposit seems to be very meagre.

Griffiths (1908), working in England, found this period to be 10 days in the case of *M. domestica*[2]; Hewitt (1910), also working in England, found it to be 14 days. Bishop, Dove and Parman (1915), working in Dallas, Texas, found the period to be only 4 days in summer and not less than 10 days in spring and autumn.

At present all that can be expected of this method is temporary local relief, such as the clearance of hospital wards, of individual rooms, etc.—and this only when fresh invaders are prevented from entering by placing muslin or wire screens over windows and doors. Such screens tend to diminish the freshness of any breeze entering, and so cause some discomfort in hot climates. Whilst trying to reduce the swarms of flies at a military hospital in Serbia, in 1915, I had to resort to method 1, owing to the lack of sufficient means to attack the breeding places successfully. I found it difficult to get some men to refrain from tearing the muslin placed over the ward windows, and impossible to get muslin-covered swing-doors, especially made for the kitchen, kept closed. The cooks, who were peasants, complained that the muslin kept out the breeze, and, not realising the danger to which they were exposing the hospital, preferred flies and breeze to no flies and less aïr; and the Commandant was not sufficiently alive to such matters to be aware of the advisability of enforcing the necessary regulations. Those wards, in which the necessary precautions were observed daily, were kept almost free from flies to the great relief of the patients.

---

[1] The period between escape from the puparium and oviposition, during which the fly becomes sexually mature and copulation takes place.

[2] *Musca domestica* forms at least 90 per cent. of the flies frequenting houses and is, therefore, the most dangerous. (Hermes, 1911, p. 521, quoted by Graham-Smith, 1914, p. 79.)

The adoption of the second method cuts nearer the root of the evil, and where suitable sanitary arrangements or efficient larvicides are available much more effective work can be done even in summer.

But, provided that suitable methods are forthcoming, winter would probably be the best season in which to attack the problem. The numbers of flies have then been reduced by natural deaths, the ravages of *Empusa muscae* and of Hymenopterous parasites, and carnivorous larvae are still taking their toll.

Portchinsky (1913) considers that the larvae of *M. stabulans* and of *H. dentipes* wreak untold havoc amongst the larvae of *M. domestica.* Graham-Smith (1916) thinks that he failed to bring the larvae of *M. domestica* through the winter of 1914–15 because those, which survived heavy rain, were destroyed by the larvae of *H. dentipes,* the progeny of a single female, which accidentally gained access to the breeding cage.

In view of supplementing the work of Nature by artificial means, it is important to discover where and in what stage, or stages, the insect passes the winter.

The writers on hibernation may be divided into four groups: Group I which holds the opinion that *M. domestica* passes the winter in the adult stage; Group II which considers that, though the adults which survive the winter are the most important factor in perpetuating the species, it is possible, but not sufficiently proved, that the pupal stage also survives; Group III which recognises that some adults do undoubtedly over-winter in suitable situations, but consider that the immature stages are of most importance in the continuance of the species in the following year; and, finally, Group IV which believes that *M. domestica* hibernates only in the pupal stage.

In Group I appear Newstead (1909) and Hewitt (1914 and 1915). The former (1907) wrote that, while the adults were found in the dwellings of man throughout the winter and in early spring, "Whether they pass the winter entirely in this stage one has not been able to ascertain. It is highly probable, however, that some of the pupae may remain over the winter and hatch in the following spring." But as a result of a single experiment, carried out in October 1907, the same observer (1909) concluded that the house-fly did not pass the winter in the larval or pupal stages—"so that as far as one can trace at the present moment, the only stage in the life cycle, which is found during the winter months is that of the adult flies." Hewitt (1912) considers that "it is not unlikely that larvae of *Fannia canicularis*, which developed late in the season, pass the winter in the pupal state, as is the case with certain *Anthomyidae*"; and (1914, p. 107) has kept *Stomoxys calcitrans* over winter as pupae; but thinks that *M. domestica* only winters in the adult stage. He points out that the abdomens of those caught in winter are full of fat and that the alimentary canal is shrivelled up. He writes (1915) that he has always held the view suggested by Copeman and Austen (1914) "that the relative lateness of the season at which house-flies annually become abundant may be due to the smallness of the numbers of individuals that in an active, or inactive condition, survive the winter in houses or buildings."

Graham-Smith (1914), summarising the opinions on this subject up to 1914, wrote that "flies may be found active throughout the winter in relatively high temperature, *e.g.* warmed houses, kitchens, bakehouses, and in the presence of sufficient food material may even continue to breed, but little is known as to their method of passing the winter under natural conditions. Most observers, however, seem to think that the winter is passed in the adult condition."

In Group II may be placed Jepson (1909) and Copeman (1913). The former considered that autumn flies were hardier than summer ones, and found them in kitchens at temperatures of 65° F.–80° F. "quite as active as in summer," and persuaded them to breed and oviposit on soaked bread. He also found sluggish specimens behind books on a bookshelf in December and January; but failed to bring 200 pupae alive through the winter.

The latter wrote "as to whether flies can persist through the winter in other than the adult form practically nothing is known; but as the eggs and larval stages, at any rate, appear to be less resistant to the effects of reduction of temperature than the fly itself, it is probable that the progeny of the later broods, for the most part, never arrive at maturity, both eggs and larvae perishing in their breeding places," and that, though it would seem that the pupae might stand the winter better than the earlier stages, he knew of no instance of their having been successfully wintered. The examination of the thatch of a hen house in March 1913, of two attics in March and May respectively, and of 25 hay and corn stacks in April showed the complete absence of *M. domestica* in those places. And Austen, who identified the specimens collected, remarked, of those which were found, that the predominance of females to males was so slight as to be practically negligible; and was not what one would expect from hibernating flies.

In Group III appear Williston (1908), Howard (1911 and 1912), Copeman and Austen (1914), Graham-Smith (1914 and 1916), Bishopp, Dove and Parman (1915) and Dove (1916)[1].

As early as 1908 Williston stated that the winter was passed in the puparia, but that in secluded spots mature flies will sometimes survive the winter. He does not, however, quote any experiments to qualify these statements.

Howard (1911) wrote that *M. domestica* hibernates "in the puparium condition in manure or at the surface of the ground under a manure heap. It also hibernates as adult, hiding in crevices": and in 1912 "Adult flies undoubtedly linger in warmed houses throughout the winter, but that enough of them remain in active condition in such locations to perpetuate the species and start the rapidly multiplying generations of the following summer seems doubtful"; but thinks it very probable that the adults do remain dormant in cold and sheltered situations. He considers that insufficient attention has been paid to the accurate identification of species found. That this may often be the case is shown by the observations of Copeman (1913) already quoted.

---

[1] Since the Preface and account of my observations on the Wintering habits of flies were written, two papers have been read, the authors of which claim to have successfully bred *M. domestica* from over-wintered pupae: and, further, certain of their observations are of interest in connection with my Burial Experiment, pp. 80–84.

I. Kisliuk (1917) found that (1) flies which are not kept cold enough to become inactive (see Dove, 1916) will either oviposit, if the temperature is high enough, or die comparatively soon; (2) under natural conditions neither eggs nor larvae are to be found alive in normally preferred situations, though the latter may probably be found in early winter (these observations were made in America, but the latter one does not tally with those made by Graham-Smith (1916), McDonnell and Eastwood (1917) and my own (1916–1917) described in this paper, when larvae of various flies were found throughout the winter). (3) From pupae collected from natural situations on February 26, a few flies emerged on March 10th–12th, though 91 per cent. were parasitised, which, he considers, indicates that *M. domestica* hibernates as a pupa. And from breeding experiments he concluded that the following species hibernate in immature stages: *L. sericata, L. caesar, L. sylvarum, Phormia regina, C. erythrocephala, C. vomitoria, Cynomyia cadaverina*, and *P. rudis*, which also does so as an adult.

II. McDonnell and Eastwood (1917) made the following observations: (1) "On March 3rd, 1917, living larvae were found in a heap of old manure at a depth of 3 *feet*. This heap had not been touched since October 1916 and was overgrown with grass and weeds. On March 20th larvae were found at a depth of 2 feet in a mixture of dry earth and human excreta, which had been made in September 1916, and was covered with a 6 inch layer of earth". (2) "Larvae found at a depth of 2 feet in a manure heap were apparently dead, but revived, when exposed to heat. Evidently they were hibernating." (3) Pupae, which had migrated from the manure in the larval state, were found 2 feet from their respective dumps at a depth of about an inch below the surface. (4) The larvae nearly all pupated within 24 hours of removal from the manure heap, but one or two were still persisting as larvae on April 14th. (5) During first week in April pupae developed into flies—*F. canicularis* and *M. domestica*.

From these observations the authors conclude that, as living fly larvae were found, in March, in earth and human excrement made six months previously, reliance cannot always be placed in the method of disposal in shallow trench latrines as a preventative of fly breeding.

In 1914 Copeman and Austen, as a result of examination of 58 consignments of flies, sent from all parts of England, only found *M. domestica* to appear 12 times, of which 9 were observations of single specimens, one of the remains of 11 dead flies (Appendix, Serial No. 4), one of several specimens reported in a baker's shop (App. Ser. No. 17), and one of a single specimen reported to have emerged from a stable manure heap near the house, from which it was thought possible to obtain several flies on any mild day throughout the winter[1].

From the results of this investigation the writers consider that the customary explanation of the perpetuation of the house-fly by overwintered adults had been fairly tested and found to fail. They therefore suggested looking for pupae during the winter in places where adults were known to have been abundant during the previous summer and autumn.

In an earlier part of the paper they suggest that the relative lateness of the season, in which the house-fly becomes abundant, may be due to the fact that only small numbers of adults overwinter, and that therefore it requires time for the numbers to increase to any importance. They remark, however, that "there is as yet nothing in the shape of proof that the female house-flies, found alive at the end of winter, actually survive until oviposition takes place." As regards this, Graham-Smith (1914) has shown that the increase in numbers of flies in autumn is closely connected with the temperature recorded by the 2 foot ground thermometer, and (1916) that the sudden disappearance towards winter is due to the non-emergence of flies from pupae, owing to the temperature falling below the critical point necessary for the emergence of *M. domestica*.

Graham-Smith (1914), though he has not actually found the pupae of *M. domestica* during the winter, records observing numerous blow-flies (*Calliphora erythrocephala*), which seemed to have freshly emerged, on sunny days at the end of February 1914, in sheltered gravel pits far from houses. In April and May 1913 he bred *Sarcophaga melanura* and *Anthomyia radicum* from samples of dog's faeces, collected in the autumn of the previous year. And, moreover, on March 28th, 1914, obtained pupae of different species from the earth near manure heaps and hatched flies from them. He summarises that the "evidence at present available seems to indicate that few house-flies hibernate as adults, and from observations on other species of flies, the writer is inclined to believe that the winter is passed in the pupal stage": but "the pupae of *M. domestica* have not yet been found." The same author (1916) found that of a few blow-flies, which emerged from pupae from time to time throughout the winter, some lived for several weeks and survived heavy rains, snow, frost, cold wind and gales; but, on the other hand, proved by experiment that the following flies hibernate as pupae, or, less commonly, as larvae in the earth, under shelter 2–3 inches below the surface of the ground or under shelter on the surface:

---

[1] Possibly the heap and its environs contained many pupae from which these flies emerged at intervals during winter, and the remainder in summer.

Calliphora erythrocephala, Mg.
Fannia manicata, Mg.
Fannia canicularis, L.
Fannia scalaris, F.
Anthomyia radicum, L.
Tephrochlamys canescens.
Blepharoptera serrata, L.
Scatophaga stercoraria, L.
Dryomyza flaveola, F.
Calliphora vomitoria, L.
Muscina stabulans, Fall.
Muscina pabulorum, Fall.
Nemopoda cylindrica, F.
Piophila vulgaris.
Hydrotaea dentipes, F.
Sarcophaga melanura, Mg.
Sarcophaga carnaria, L.
Stomoxys calcitrans, L.
Mydaea lucorum, Fall.
Lucilia caesar, L.
Lucilia sericata, Mg.
Phaonia erratica, Fall.
Ophyra leucostoma, W.
Polietes lardaria, F.

and considers that "a few individuals, insignificant in number compared with those passing the winter as pupae, hibernate in the adult condition" but that, in perpetuation of the species, these are of little account; yet "the wintering habits of *M. domestica* are still obscure."

Bishopp, Dove and Parman (1915) at Dallas and Uvalde, Texas, found that the winter could be passed in the immature stages, and, moreover, none of the adults under observation survived the winter. Their results indicate that flies kept at a temperature not low enough to render them inactive, either oviposited very soon or died[1]. They think the chances of adults finding shelter from destruction by cold very small indeed, and that, although some adults may hibernate thus, the species is dependent on those individuals which winter in the immature stages or continue to breed throughout it.

Dove (1916) found that larvae and pupae of *M. domestica* overwintered as such at Dallas and at Uvalde, Texas, and emerged on mild days in winter at temperatures below 45°–55° F. When fresh manure was not added to the experimental heap emergence ceased owing to the fall of temperature, which had been kept up by fermentation. But he thinks that pupae, which were located near the surface of the soil, received either enough heat for emergence or were probably killed by cold. He found that flies tend to seek a temperature of 60° F., but that, given that they had sufficient food, their only chance of living for any length of time was to remain dormant. He suggests, as the result of a single experiment, that *Empusa muscae* developes principally in sexually matured and fertilised females, which do not oviposit on account of cold or lack of suitable media.

---

[1] Vide Dove's (1916) suggestion, quoted later, that *E. muscae* chiefly attacks mature females which have not oviposited.

Finally Group IV is represented by Skinner (1913), who observed fresh specimens of *M. domestica* entering his laboratory window on March 13th, 1913, and states that, until disproved, he will answer the question "Do flies hibernate?" thus, "house-flies pass the winter in the pupal stage and in no other way."

At the suggestion of Dr Graham-Smith, a careful examination of manure heaps and their vicinities and other likely places, for larvae and pupae, was started in January 1916, and was continued during the winter 1916–1917. During the summer of 1916 and the early portion of that of 1917 various experiments and observations were made, a full account of which will be found in the Cambridge University Library (*Research Student's Dissertation*, 166). In this paper a short account only is given of observations made on overwintering and summer distribution of flies; and of three of the experiments, carried out during the summer, to investigate (1) the temperature of horse manure heaps; (2) the effect of applications of Creosote Oil Mixture and the best method to apply it; and (3) to discover whether the burial of material infested by the fly larvae, at a depth of four feet, would prevent the developement or escape of the adult, where the larvae would pupate under these conditions and to what height the adults were capable of climbing in various soils, loose or tightly packed.

This work was carried out on a grant from the Medical Research Committee and under the direction of Dr G. S. Graham-Smith, to whom my sincere thanks are due for his ever ready help and encouragement throughout the investigation. My thanks are also due to Mr Forman for much help and suggestion in the designing of apparatus in Series 3 (facing pp. 69, Figs. 1, 2, and 70, Figs. 3, 4), and to Mr C. G. Lamb and to Dr Keilin for their kindly help and sympathy and for identifying certain of the flies caught or bred during the experiments.

WINTER OBSERVATIONS.

The winter search for flies in immature stages in natural situations was started in January 1916 and was continued during the whole winter of 1916–1917. Between January 27th and April 20th, 1916, 14, and between September 22nd, 1916, and April 23rd, 1917, 31 likely places were examined, 45 in all. Of these, 13 were horse manure heaps or near horse manure; 12 were in or near cow manure heaps; 4 in or near horse and cow manure mixed; 6 in or near pig manure; 1 in fowl manure; 3 in ash middens; 1 in a refuse pit; 1 a town road-scrapings tip; 1 in ground in corner of a slaughter-house yard; 1 in soil under a spot over which human faeces had been exposed during the previous autumn; 1 in soil under a spot over which cow manure had been similarly exposed; and 1 in the nests of House-martins and Pigeons in an old mill.

Thirty-seven of these places were in Cambridgeshire, 7 in Norfolk and 1 in Argyll: 29 were in the country and 16 in the town of Cambridge.

Besides the larvae and pupae collected from these sources, some were taken from cow manure and others from the neighbourhood of horse manure, which had been exposed during the previous autumn in the course of other experiments.

The only observations of this nature heretofore recorded are those of Graham-Smith (1914 and 1916) and of Bishopp, Dove and Parman (1915). The former examined soil near manure heaps in Cambridgeshire, England, on March 28th, 1914, and, in damp soil under a hedge near one heap, at a depth of about 6 inches, found several pupae of *Calliphora erythrocephala* and one of *Ophyra leucostoma*; and "in soil close to another heap, which was situated in an open field" a number of pupae from which *Anthomyid* flies eventually emerged.

Bishopp, Dove and Parman, working at Dallas and Uvalde, Texas, found considerable numbers of House-fly larvae in chicken manure in poultry houses in mid-winter, where they consider the conditions "especially favourable for the immature stages to pass the winter, as the manure generated very little heat, yet being within the chicken house the insects are not subject to excessive cold." They also found great numbers of larvae in Livery barns, which furnished similar conditions, "in cracks in the floors and in corners of the stalls."

Methods employed.

The larvae were always taken to the laboratory in some receptacle supplied with holes to admit a plentiful supply of air, placed in jam jars (size 1–2 lb.) and given a little of the manure in which they had been found—when this material was very moist a little dry earth was added to tempt them to pupate.

Throughout the investigation it was found very difficult to overcome the efforts of the larvae to migrate from the jars, in which they were confined. A glass filter funnel was dropped into the mouth of each jar, thus at once closing it and admitting air. However, in spite of this, some larvae did either find a spot where some irregularity in the rim of the jar permitted them to squeeze between it and the filter funnel, or actually made their way up the inside of the funnel. Very few managed this gymnastical feat, and the first path of escape was effectually blocked later by a layer of plasticine.

The temperatures recorded were taken with an ordinary centigrade thermometer placed in a large glass tube, held in position by a piece of cork, and surrounded at the bulb end by paraffin wax. The bulb end of the glass tube was closed with a cork, the opposite end being left open. This device, though prolonging the time necessary to leave the thermometer in the manure, enabled the temperature to be read before the mercury fell on the withdrawal of the tube from the heap.

A table giving the species found in the larval or pupal stages, from which adults were actually bred, is given; those which are additional to Graham-Smith's (1916) list being marked; the kind of manure in which each species was found, the dates of findings and the sexes, which emerged, are also shown (pp. 64, 65).

Summary of observations.

1. Thirty-nine species were actually bred from larvae or pupae found in natural situations during the winter; 31 of these are additional to Graham-Smith's (1916) list.
2. Larvae of *Dolichopodidae* were found in soil near cow manure, and were identified by Dr D. Keilin, but were not successfully reared.
3. Pupae of *Musca domestica* were found during winter in horse manure but the adult was not reared.
4. It is possible that larvae and pupae of other species were found, though they were not successfully reared.
5. The distribution of dipterous larvae in a manure heap in winter, in the Eastern Counties, is extremely local. Similar observations were made at Dallas and at Uvalde, Texas, by Bishopp, Dove and Parman (1915), but they do not state whether their observations referred to both summer and winter, or to either period in particular.

TABLE I.

List of Flies actually bred from Larvae and Pupae collected during the Winters 1915–1916 *and* 1916–1917.

Flies marked with * are additional to Graham-Smith's (1916) list.

	Fly	Horse Manure	Cow Manure	Horse and Cow Manure	Pig Manure	Fowl Manure	Dates on which found	Sexes emerged	Dates of Emergence
1	*Sciara* sp.*	LLL (?)	—	—	—	—	19. iii; 6. iv. 17	—	25–30. iv. 17
2	*Scatopse notata**	L	—	—	—	—	2. iii. 17	—	22. iv. 17
	,, ,,	—	—	—	LL	LLPP	27. iii.; 6. iv. 17	8 ♂ 5 ♀	26. iv. & 2. v. 17
3	,, sp.*†	—	—	—	—	LL	—	—	—
4	*Dilophus febrilis**	—	—	LLL	—	—	24. iv. 16	27 ♂ 35 ♀	—
5	*Bibio hortulanus**	—	—	LLLL	—	—	5. iii. 17	♂s ♀s	29 and 30. v. 17
6	*Bibio Johannis**	—	LL	—	—	—	29. i. 16	1 ♂ 1 ♀	—
7	*Psychodidae**	—	L (?)	—	—	—	—. i. 17	—	6. iv.–1. v. 17
8	*Tipula* sp. 1*	L	—	—	—	—	12. ii. 16	—	—
9	,, sp. 2*	—	LL	—	—	—	28. ii. 17	—	1. v. 17
10	*Rhyphus fenestralis**	—	LLL	—	—	—	7. x. 16	—	1–28. v. 17
11	*Sargus cuprarius**	—	LLL	—	—	—	29. ii.; 3. iii. 16	♂s ♀s	June and July 16
12	*Chloromyia formosa**	L	—	—	—	—	March	1 ♀	—
13	*Microchrysa polita**	—	LL	—	—	—	3. iii. 16	3 ♂ 1 ♀	—
14	*Ascia podagrica**	LL	—	—	—	—	2. iii. 17	3 ♂ 1 ♀	28 & 30. iv. & 5. v .17
	,, ,,	—	LL	—	—	—	29. ii. 16	3 ♂ 1 ♀	—
15	*Eristalis tenax**	L	—	—	—	—	12. ii. 16	—	July 1916
16	,, *arbustorum**	—	L	—	—	—	1. i.; 26. ii.; 2. iii. 17	1 ♀	18. iv. 17
17	*Syritta pipiens**	—	LLL	—	—	—	29. ii. to 22. iii. 16	♂s ♀s	13–18. v. 17
	,, ,,	—	LL	—	—	—	22. ix. 16; —. i.; 23. iv. 17	3 ♂ 1 ♀	—
18	*Tachina* sp.*	—	—	—	—	—	21. viii. 16 .	1 ♀	14. v. 17‡
19	*Stomoxys calcitrans*	—	—	—	LLPP	—	7. ii. 16	1 ♀	—
20	*Graphomyia* sp.*	—	L	—	—	—	24. iii. 16	1 ♀	—
21	*Crytoneura caesia**	—	—	—	L	—	7. iii. 17	1 ♀	7. v. 17
22	*Morellia hortorum**	—	PP	—	—	—	—. ix. 17	15 ♂ 5 ♀	7–13. v. 17§

23	*Calliphora erythrocephala*	—	—	—	—	—	25. x. 16	♂ ♀	Jan. 1917‖
	,, ,,	—	—	—	—	—	1. i. 17	♂ ♀	9. ii. 17¶
	,, ,,	—	PP	—	—	—	—. i. 17	1 ♂	4. v. 17
24	*Hydrotaea dentipes*	—	LLPP	LLPP	LLLPPP	—	1. ii.; 13–23. iii.; 20. iv. 16	40 ♂ 28 ♀	—
	,, ,,	—	—	—	LLL	—	—. ii. to 7. iii. 17	6 ♂ 3 ♀	30. iv. & 2. v. 17
25	*Anthomyia radicum*	—	P	—	—	—	1. ii. 16	1 ♂	—
26	,, sp. 1*	P	—	—	—	—	2. iii. 17	1 ♂	30. iv. 17
27	,, sp. 2*	—	PP	—	—	—	—. ix. 16	—	9. v. 17
28	*Chortophila cinerella**	—	PPP	—	—	—	7. x. 16	♂ ♀	28. iii. & 16. v. 17
29	*Pegomyia socia**	—	P	—	—	—	22. ii. 17	—	30. iv. 17
30	*Fannia manicata*	—	—	—	—	LL	6. iv. 17	♂s ♀s	May 17
31	,, *scalaris*	LLL	—	—	LLL	—	—. 29. ii.; 13–22. iii. 16	125 ♂ 73 ♀ (26?)**	—
	,, ,,	—	—	—	LL	LLPP	6. iv.; 27. iii. 17	♂s ♀s	6. iv. 17
32	,, *canicularis*	—	—	—	LL	LLPP	6. iv. 17	♂s	6. v. 17
33	*Scatophaga stercoraria*	—	PP	—	—	—	29. i. 16	3 ♂s	4. v. 17††
34	*Tephrochlamys rufiventris**	—	—	PP	—	LLPP	22. iii. 16; 22. iii. 17	—	9–16. v. 17
35	*Lonchaea vaginalis**	—	PPLL	—	L	—	20. iv. 16	1 ♂ 3 ♀	7, 14 & 21. v. 17
							7. iii.; 28. iv. 17	1 ♀: ♀s ♂s	
36	*Sepsis* sp.*	—	PP	—	—	—	—. ix. 17	—	7–9. v. 17
37	*Borborus equinus**	aaaPP	aaaaPPPP	—	—	—	—	—	Throughout winter
38	*Limosina sylvatica**	—	LL	—	—	—	—. i. 17; 19. ii. 16	1 ♂	—
	,, ,,	—	—	P	—	—	22. x.; 23. iii. 17	2 ♂ 3 ♀	17. iv. 17
39	*Stenopteryx hirundinis**	—	—	—	—	—	25. x. 16	♂ ♀	12 & 14. v. 17‡‡

a, P or L denote the stage in which the insect was found, a = adult, P = pupa, L = larva. aa = a few adults, aaa = many adults, aaaa = very many adults.

† No sign of *Scatopse* larvae was seen when manure was first collected but they appeared later in the closed jam jar in the laboratory; it is possible that either eggs or very small larvae were in the manure provided for *T. rufiventris* but were not noticed.

‡ From cocoons of small Ermine moth (*Hyponomeuta* sp.). § (All females on 13. v. 17.)

‖ From Martins' nests. ¶ From soil in corner of slaughter-house yard. PPLL.

** 26 *F. scalaris* were destroyed and so it was impossible to determine their sex.

†† From human excrement, which had been exposed during autumn 1916. PPP.

‡‡ Reared separately by Mr N. D. F. Pearce and self from pupae found in Martins' nests.

Consequently the futility of calculations based on the number of larvae or of pupae per pound of manure is apparent.

6. In the majority of manure heaps, examined during the winter, there was no evidence that the larvae preferred any particular part of the heap; but in a few cases they seemed to show a slight preference for those portions which received least light.

7. On February 19th and 29th and on March 4th, 1916, several Chelifers—*Chernes nodosus*—were found in dryish cow manure, at a spot in the heap which registered a temperature of 35° C. On March 4th some were carrying their egg-masses. Large numbers of *Gamasid* mites were also found in the same heap.

8. The following parasites were bred—from two pupae of *Hydrotaea dentipes,* found in cow manure, 2 *Ichneumons* (*Atractodes tenebricosus,* Grav. ♀, *A. exilis,* Hal. ♂); from a third pupa of *H. dentipes* a *Figitid*; from pupa of *Lonchaea vaginalis* or of *Anthomyia radicum* an *Ichneumon*; from 2 *Calliphora*-like pupae, found in an ash midden, 1 and 2 *Figitids* respectively; and from 3 pupae of *Eristalis tenax* 72 (10 ♀ and 62 ♂), 24 and 8 (5 ♂ and 3 ♀) *Proctotrypids—Diapria conica,* Fabre, were extracted dead (see Kieffer and Marshall, 1907, pp. 948–950).

OBSERVATIONS ON THE DISTRIBUTION OF FLIES DURING THE SUMMER AND AUTUMN 1916.

From July to September a certain number of places were visited to ascertain whether the House-fly and other species were present, and whether distance from a town or other houses affected the species or numbers of *Musca domestica.*

In some cases old fly papers and contents of traps were collected and fresh fly papers hung up; in two instances traps were set and baited; and in all cases flies present were caught and examined.

For this purpose the places examined were divided into five groups:

(*A*) = Places in town (Cambridge).
(*B*) = Places, other than houses, outside town near buildings.
(*C*) = Places, other than houses, outside town far from buildings.
(*D*) = Houses far from buildings.
(*E*) = Houses near buildings.

(*A*) During the summer the majority of *M. domestica* were found in the neighbourhood of horse manure, and were found to linger longest in artificially heated buildings, *e.g.* a bakery. The latest date on which a house-fly was found in the former situation was December 2nd, on which day one was found, and in the latter situation, resting high up on the wall of a top-floor room and only moving on compulsion, December 9th.

(*B*) *M. domestica* was only found near horse manure except on two occasions—once in large numbers on moist brewer's grains in the troughs in a cow-house; and once a single female on rotting vegetation near a house on July 22nd. The majority of Diptera were *Stomoxys calcitrans*, *Scatophaga*, *Borborus equinus* and *Limosina* sp.

On one farm it was very noticeable that when the cows were brought in for milking in the afternoon they became very restless for the first five minutes after entering their stalls, kicking and lashing their tails. During this period no *Stomoxys* were to be seen in the sun on the cow-house wall outside; but afterwards, when the cows had become quiet, this wall was covered with *Stomoxys* freshly filled with blood.

(*C*) *M. domestica* was not found. The majority of Diptera found were *Scatophaga* sp., *Sarcophaga* sp., *Stomoxys* sp., *Borboridae* and *Anthomyidae*.

(*D*) Most of these houses were examined too late in the season to judge of fly prevalence in summer. One, examined on October 12th, had *Fannia canicularis* only. Traps set up in two derelict houses in Southery Fen, where 30,000 acres had been under water for 9 months—June 3rd, 1915 to September 1915, and again from May 1916 to December 1916—attracted 2 female *M. domestica*, 1 female *Stomoxys calcitrans*, 1 male *P. rudis* and 4 *C. erythrocephala*. The last mentioned laid eggs on the baits—human faeces, plums, milk and sheep's noses, which were placed together in the same receptacle.

Both houses were ¼ mile from the next derelict building; and one was ½ and the other 2 miles from land. Two of the four *C. erythrocephala* caught were found at the former house, the remainder at the latter.

During the interval between the two floods search of the fields for insect life resulted in finding only the larvae of *Chironomomus*, one *Syrphid* larva and a boring beetle grub—the latter being found in a post above water level.

Earthworms were only found in straw stacks, where leech cocoons were also found during the second flood.

During the second flood large numbers of Capsids were seen on isolated clumps of Willows surrounded by water.

(*E*) Large numbers of *M. domestica* were seen in farm houses during the summer, and many were caught in them and in a few cottages in October. On November 9th and 23rd a few were seen in the kitchen of a farm house.

A clean cottage had no flies, whilst one, to which it was attached and which was less clean, had many *M. domestica.* No flies were found on November 29th in a cottage, in which there had been large numbers on the 6th.

M. domestica was, therefore, found in largest numbers in town and in the country in the neighbourhood of horse manure—in the latter case in and about farmyards and buildings and in warm kitchens of farm houses. But the numbers were found to decrease markedly when isolated houses in the country or manure heaps far from buildings were examined. In farmyards and manure heaps far from buildings in the country such genera as *Stomoxys*, *Scatophaga*, *Borborus* and *Limosina* predominated.

M. domestica was observed alive in town as late as December 2nd outside, and December 9th inside; in the country as late as December 4th both outside and inside in 1916. In 1917 a house-fly was caught in a house in a village in Cambridgeshire during the last week in December, so that it is probable that those seen in that month in 1916 lingered sometime longer, but the places were not revisited in that year.

OBSERVATIONS ON A HORSE MANURE HEAP IN SUMMER.

Observations were made on the temperature generated in a horse manure heap; the number of flies emerging therefrom; its attraction for adult flies and power to nourish their larvae after fermentation; and on a preliminary trial of the effect of an application of creosote oil mixture (see Forman and Graham-Smith (1917), pp. 123–199).

From July 31st to October 21st, 1916, three separate experiments—*A*, *B*, *C*—were carried out; each dealing with about 6 cwt. of horse manure, which was one day's accumulation from a stable in Cambridge.

The manure was, in each case, made into a heap in a specially prepared enclosure; and daily observations were made on temperatures recorded at certain points in the heap, on the number of flies emerging from it and the time of their emergence.

Experiment *A* dealt with 6 cwt. 1 qr. manure, and lasted from July 31st to August 14th. The manure was thrown into a loose heap. Experiment *B* dealt with 6 cwt. of manure which was tightly packed, and lasted from August 31st to October 29th. Experiment *C* dealt with 5 cwt. 1 qr. manure, which was loosely thrown up as in *A* but treated "incrementally[1]" with 1225 c.c. of creosote oil mixture. It lasted from September 18th to October 21st.

---

[1] This term implies that the manure was spread out in a thin layer upon the ground and the fluid then sprayed evenly over its surface.

Method.

A wooden enclosure was made 6′ 6″ × 7′, three sides of which were formed by a tray 4″ wide (Fig. 1 *LMQJ* and Fig. 2 *MKRP*), having an outer wall extending 1′ above and 6″ below ground. This tray was filled with sawdust and protected from wet by a sloping roof (Fig. 2 *MN*). The walls were sunk below the ground level to prevent the larvae from migrating, and the sawdust was to persuade them to pupate within the enclosure. The fourth side was closed by a hollow wall 3′ 6″ high, the inner side of which was sunk 6″ below the ground (Fig. 1 *DLIJ*). The 4″ between the back and front boards (Fig. 1 *GHDI*) was filled with sawdust to act as a non-conductor; and the wall was pierced in a centre line by five ½″ holes at points 3″, 6″, 12″, and 18″ from a point 2′ 6″ from the ground, which was to be the top of the heap.

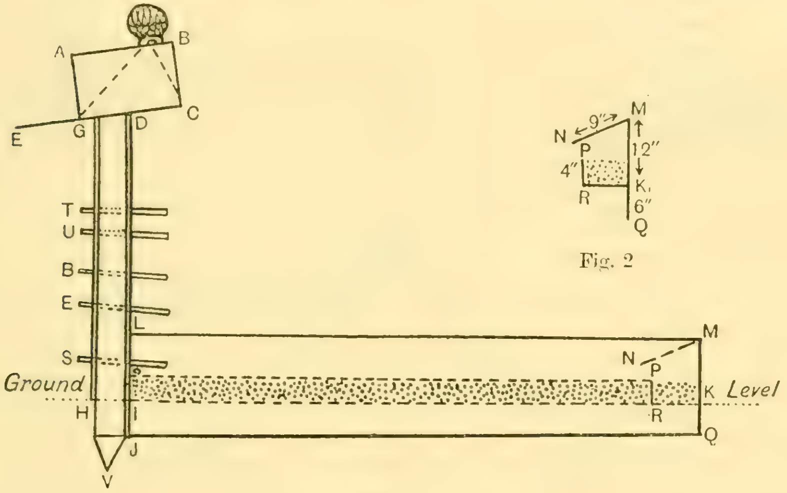


Fig. 2

Fig. 1.

Dotted Area = Sawdust.

The manure was placed against this wall so that its upper surface reached this point 2′ 6″ from the ground. Tin tubes, closed at one end, were then inserted through these holes so that they projected 6·5″ into the heap. Temperatures were taken by inserting a centigrade thermometer into each tube. The thermometer used could be read without removing it from the tube; and was provided with a piece of rubber tubing which fitted on to the open end of the tin tube into which it was inserted, thus preventing warm air from escaping from the tube. When the tubes were empty their outer ends were closed with rubber corks. In this way temperatures were taken daily at several points in the heap without disturbing the manure. The thermometer was left in each tube for 10 mins.—the temperature becoming constant in that time.

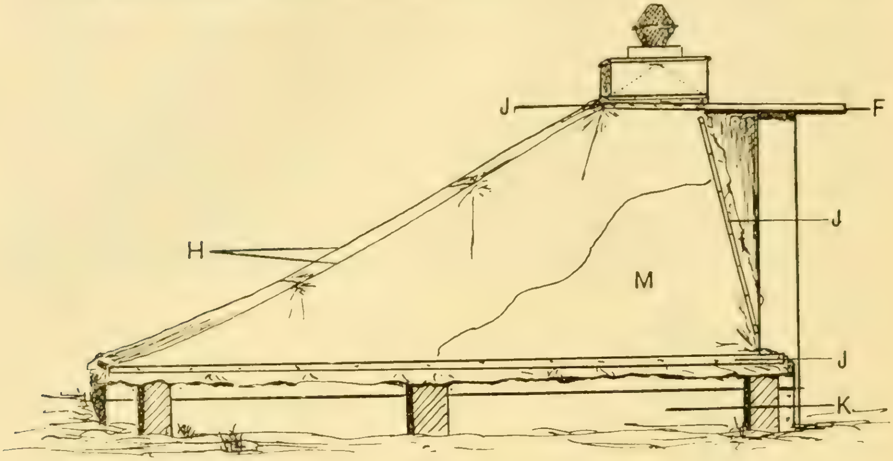


Fig. 3.

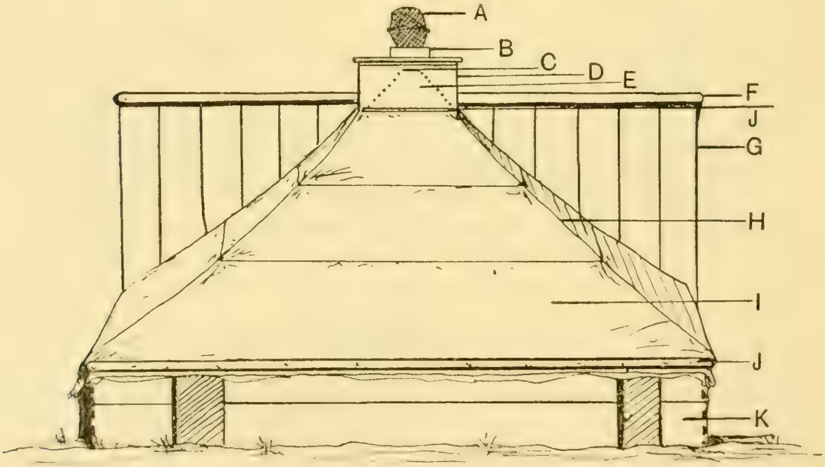


Fig. 4.

Figs. 3, 4. *A*, balloon trap: *B*, wooden square with hole in centre to hold trap: *C*, lid of tobacco tin (with hole in centre) to catch muslin: *D*, square wooden box: *E*, muslin, soaked in black ink caught under tobacco tin and at sides of box: *F*, roof to shelter thermometers: *G*, wooden wall against which manure was placed: *H*, support wires: *I*, muslin: *J*, lath, holding muslin: *K*, outside of tray containing sawdust (Figs. 1, 2): *M*, manure.

In order to collect the flies which emerged, the heap was enclosed by means of muslin supported on wires (see Figs. 3 and 4) so arranged that all sides sloped to an inverted box. Inside this box a muslin funnel was constructed by nailing muslin to the sides and pulling it down to the centre by catching it between the bottom of the box and the lid of a round tobacco tin. Thus all the flies were guided to a small skylight at the end of the muslin funnel, over which was set a balloon trap.

In order to find out whether manure, which had almost ceased to ferment still had attraction for adult flies or nourishment for their larvae, a sample of horse manure was taken from a heap when it had ceased to ferment. Part of this was placed in a large biscuit tin, provided with a very fine gauze-covered hole in the lid to admit air, into which 66 half-grown larvae of *M. domestica* were placed. On September 28th 8 pupae were found, from which only one *M. domestica* emerged. From another portion of the sample a water extract was made by soaking it in a bucket of water for 36 hours, stirring at intervals, straining the liquid through coarse muslin and evaporating it over a waterbath to the consistency of rather liquid porridge. A watch glass containing some of this extract was then placed in a cage with 36 *M. domestica* (9 ♂ and 25 ♀) which had been fasted for a week. They took practically no notice of it and were all dead in about 10 days.

Summary of observations.

The results of the three experiments may be summarised thus:

1. In a loosely formed horse manure heap the maximum temperature is reached during the first 3 days from the time the heap is formed, provided that the manure is not more than 24 hours old when so treated; and subsequently a fairly rapid and steady fall takes place throughout the heap. This may be influenced, to some extent, by external temperature (Chart I).

2. In a tightly packed heap the temperature registered by the superficial portions resembles the temperatures recorded throughout a loosely packed heap. On the other hand, the deeper portions tend to remain at high temperature for a long time and then to fall suddenly (Chart II).

3. A comparatively lower mean temperature and a quicker fall was registered in experiment *C* than in either experiments *A* or *B*. In the former case they were due chiefly to a corresponding decrease in the temperature of the air, but in the latter case chiefly to the fact that the mean temperature of the manure in experiment *B* was kept relatively

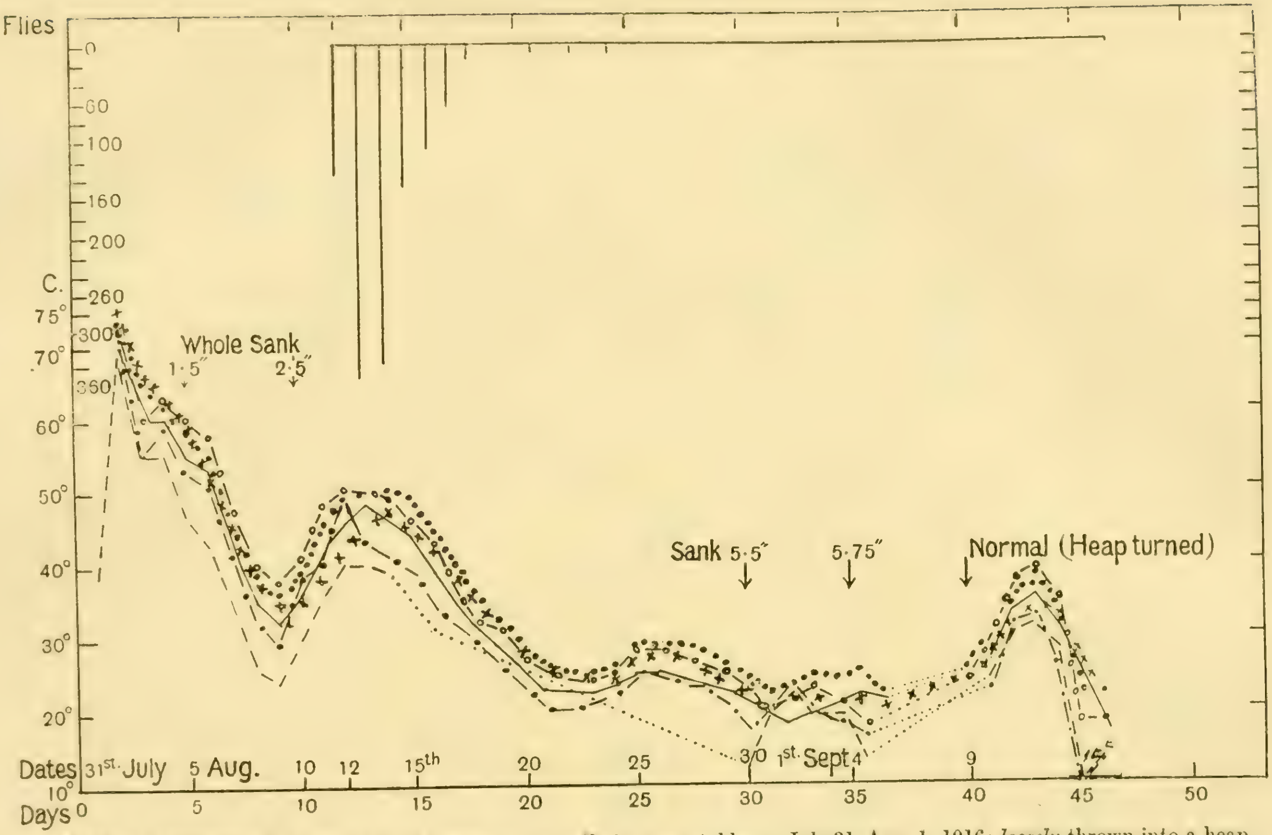


CHART I. *Experiment A.* 6 cwt. 1 qr. of horse manure made in town stables on July 31–Aug. 1, 1916: *loosely* thrown into a heap on Aug. 1. Temperature taken first on Aug. 2: heap exposed till Aug. 10, then enclosed with muslin. Flies came out between Aug. 12 and 23—total 1142, of which 1132, *i.e.* 99 per cent. were *Musca domestica* (48 per cent. ♂, 52 per cent. ♀). Heap sank a little as marked.

Curves of average daily temperature at points 6″ into back of heap.

————————	Mean of all five curves
— — — — —	Hole 1 at commencement 3″ from top of heap
—.—.—.—.—	,, 2 ,, ,, 6″ ,, ,,
—o—o—o—o—	,, 3 ,, ,, 12″ ,, ,,
....	,, 4 ,, ,, 18″ ,, ,,
× × × × × × ×	,, 5 ,, ,, 24″ ,, ,,

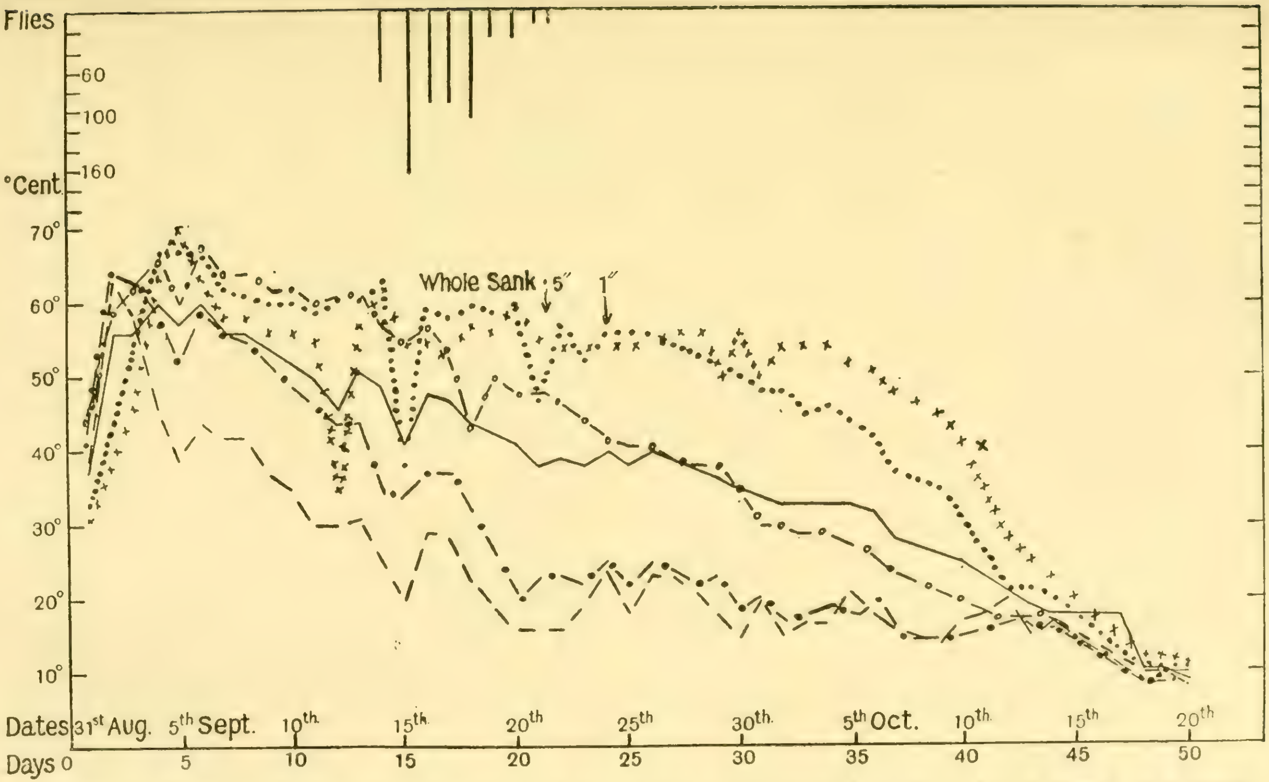


CHART II. *Experiment B.* 6 cwt. horse manure from same source as in Experiment *A*: made on Aug. 31–Sept. 1, 1916: *tightly* packed into a heap on Sept. 1. Temperature taking started Sept. 1, finished Oct. 20. Heap enclosed Sept. 13. From Sept. 14 to 29 678 flies caught—673 were *M. domestica*, 99 per cent. (45 per cent. ♂, 55 per cent. ♀). Heap sank a little as marked.

Curves of average daily temperatures at point 6″ into back of heap and curve of mean of all five.

————————	Mean of all five curves					
— — — — —	Hole 1	at	commencement	3″	from	top of heap
—.—.—.—.—	,, 2	,,	,,	6″	,,	,,
—o—o—o—o—	,, 3	,,	,,	12″	,,	,,
....	,, 4	,,	,,	18″	,,	,,
× × × × × × ×	,, 5	,,	,,	24″	,	,,

high by packing and possibly, to a much less extent, to the mean of *C* having been reduced by the effect of creosote oil mixture on fermentation (Chart III).

4. The flies began to emerge about the 12th day, the majority appeared in 5 days; the period of emergence lasted about a fortnight. 2083 of the flies, which emerged in all three experiments, were caught in the trap and counted; 99·5 per cent. of these were *Musca domestica* (1141 in *A*, 680 in *B*, and 262 in *C*).

5. Male *M. domestica*, as a whole, started emerging rather sooner than the females.

6. Creosote oil mixture when sprayed incrementally at the rate of a gallon to the ton of horse manure did not entirely inhibit developement of flies. But as these experiments were not carried out simultaneously, it was not possible to judge of its precise effect from this experiment (see pp. 78–80).

7. Horse manure, which has almost finished fermenting and is cold, has probably no attraction for adult house-flies, and very little nourishment for their larvae, though larvae of other species have been found therein throughout the winter and flies, in some cases, successfully reared.

(For Temperature Curves see Charts I, II, III.)

A further Experiment to Discover the Amount of Creosote Oil Mixture necessary to spray upon Manure to Prevent Developement of Flies, and the best method of Application.

On February 26th, 1916, one day's production of horse manure, procured from the same source as for the previous experiment, was divided into five lots of 1 cwt. each. Each lot was then spread out separately in a stable yard in layers about a foot deep, to allow of a possible re-infection by flies. After 4 days exposure each plot was wetted with half a bucket of water to make it about as damp as when first spread, packed into tubs (Fig. 5) and treated as below:

No. of Tub	Treatment
1 (control)	Packed down tightly
2	Packed down tightly and sprayed on surface with fine spray with 218 c.c. Creosote Oil Mixture = 1 gallon to 1 ton
3	Packed down tightly and sprayed on surface with fine spray with 873 c.c. Creosote Oil Mixture = 4 gallons to 1 ton
4	Packed down tightly and sprayed "incrementally" with fine spray with 218 c.c. Creosote Oil Mixture = 1 gallon to 1 ton
5	Packed down tightly and sprayed "incrementally" with fine spray with 873 c.c. Creosote Oil Mixture = 4 gallons to 1 ton

On October 2nd several larvae of *M. domestica* were seen on the inside of the control tub, escaping from the excess of heat. The temperature about 6 inches below the surface was, at that time, about 67° C. No life was apparent in the other tubs. On October 3rd many very small flies and a few *Psychodidae* were seen inside the muslin covering the control, and very many very small larvae were seen energetically writhing at the ends of protruding straws, as if trying to escape from the heat below; a dead beetle was found on No. 4 and a few live beetles on the remainder. On October 11th 1 cwt. horse manure, procured from the same source and treated in a similar way to the first 5 lots, was placed in tub No. 6 and sprayed "incrementally" with a solution of borax (1 oz. borax, 1 qt water: 1 cu. ft manure).

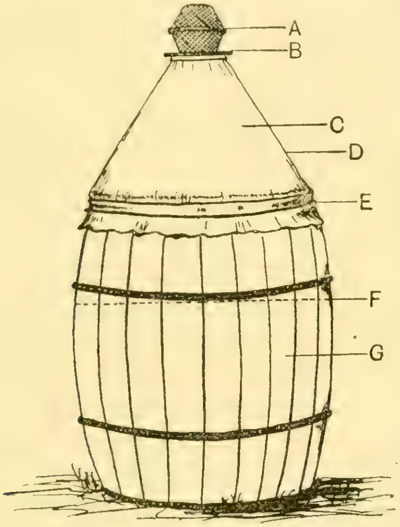


Fig. 5. *A*, balloon trap: *B*, wooden square with hole in centre supported by four wires fastened into hoop inside tub: *C*, muslin: *D*, supporting wire: *E*, tape to hold muslin: *F*, surface of manure (1 cwt.): *G*, wooden tub.

On the first 5 days tubs 2, 3 and 4 gave higher temperatures than the control; but No. 5, which had been sprayed incrementally at the rate of 4 gallons to 1 ton, showed a lower temperature on the first three days and a higher on the fourth and fifth. This seems to suggest that Creosote Oil Mixture, when applied to the surface, tends to retain the heat generated below, so that the heap takes longer to cool; but that if applied incrementally in sufficient quantity, fermentation is delayed and the temperature rises more slowly (Chart IV).

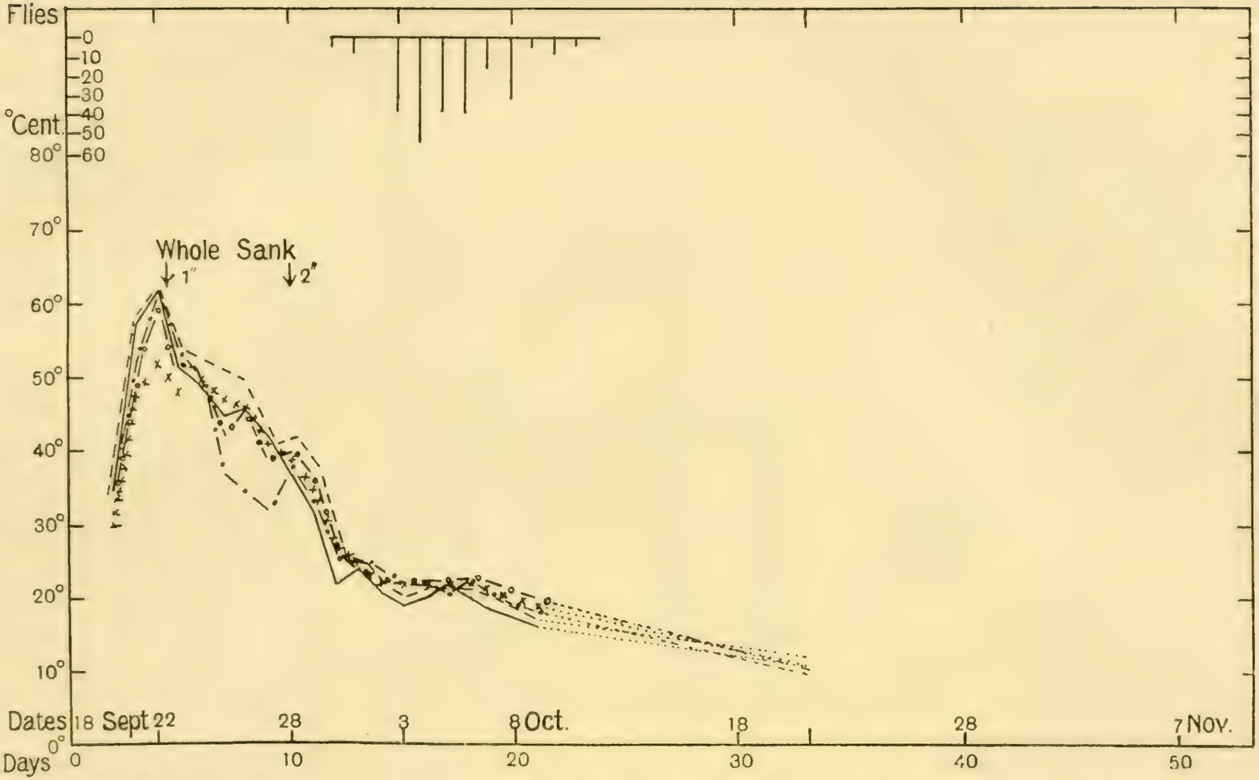


CHART III. *Experiment C.* 5 cwt. 1 qr. of horse manure made in town stables on Sept. 18–19, 1916: brought to School of Agriculture on Sept. 19 and spread out to a depth of a few inches: sprayed by means of a hand syringe with 1200 c.c. of creosote oil mixture, *i.e.* 1 gallon to 1 ton. (50 c.c. were sprayed on surface on which heap was to rest: the manure was spread in quarters, each receiving 250 c.c., leaving 150 c.c. for surface of heap. An extra 25 c.c. was added because of wind.) 312 flies emerged between Sept. 30 and Oct. 14. Later heap sank a little as shown.

Curves of averages of daily temperatures at five points 6″ into back of heap and, at beginning of experiment 3″, 6″, 12″, 18″ and 24″ from top of heap.

————————	Mean of all five curves					
— — — — —	Hole 1	at commencement		3″	from top of heap	
—.—.—.—.—	,, 2	,,	,,	6″	,,	,,
—o—o—o—o—	,, 3	,,	,,	12″	,,	,,
....	,, 4	,,	,,	18″	,,	,,
×××××××	,, 5	,,	,,	24″	,,	,,

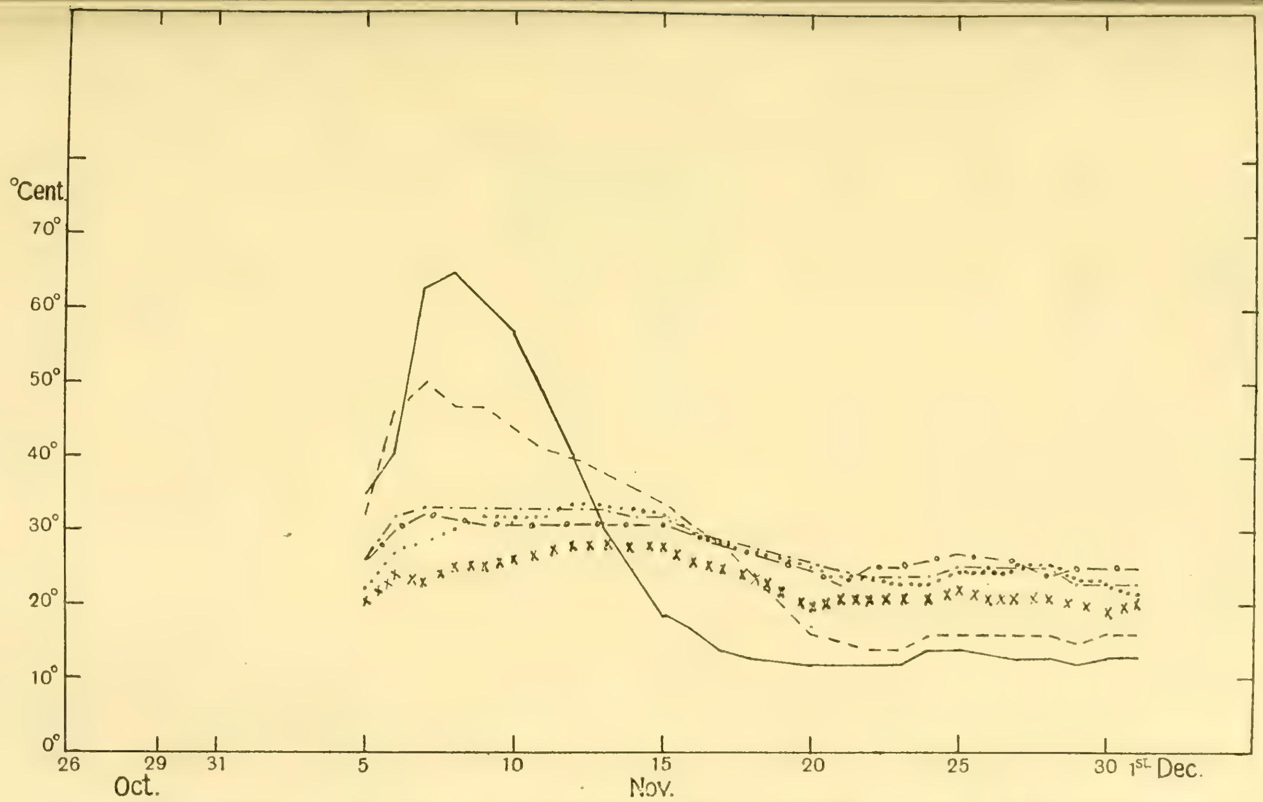


CHART IV. *Experiment. Curves showing the daily average temperature of the manure in each tub, as registered at points 3″, 6″ and 12″ from the surface.*

Treatment of manure in each tub.

1. Control, only pressed

"Incrementally" {
2. Sprayed with creosote oil mixture (2 galls to 1 ton)
3. " " " (4 galls to 1 ton)
4. " " " (8 galls to 1 ton)

Surface {
5. Sprayed with borax (at 1 oz. to 1 qt of water to 1 cub. ft manure)
6. " " " " " " "
then sprayed with creosote oil mixture (1 gall. to 1 ton)

——————— 1 —.—.—.—.— 3 5
— — — — — — 2 —o—o—o—o— 4 × × × × × × × 6

A little life was evident in all five tubs on the first three days; but, whereas the control gave 81 *M. domestica* between October 10th and November 13th, No. 2 (surface 1) gave 1418, No. 3 (surface 4) 130, No. 4 (incrementally 1) 3, and No. 5 (incrementally 4) 2; whilst No. 6 (borax) gave 16.

The difference between the flies emerging from the control and from tub 2 may have been due to uneven sampling of the manure. Nevertheless the figures 2 and 3 contrast sufficiently with those of 81, 1418 and 130 to justify the following suppositions:

1. That the larvae are able to live between the great heat generated below by the manure and the larvicide sprayed on the surface only. (The temperature 1 in. below was 41° C. on the fifth day, *i.e.* when the manure was 19 days old.)
2. That the best method to apply Creosote Oil Mixture is "Incrementally."
3. That 1 gallon to the ton is sufficient; but a previous trial indicated that more is needed.

As the first experiment seemed to show incremental spraying to be more effective than surface treatment, it was decided to repeat the experiment with variations in quantities of solution, and to make a further trial of borax.

On October 30th, 1916, horse manure procured from the same source was thoroughly mixed to ensure even sampling, divided into six lots each of 1 cwt. 1 qt. and exposed as before. On November 20th they were treated as follows:

1. (Control) pressed into tub.
2. Sprayed incrementally with 436 c.c. Creosote Oil Mixture = 2 gallons to 1 ton and pressed into tub.
3. Sprayed incrementally with 872 c.c. Creosote Oil Mixture = 4 gallons to 1 ton and pressed into tub.
4. Sprayed incrementally with 1744 c.c. Creosote Oil Mixture = 8 gallons to 1 ton and pressed into tub.
5. Watered with can with 5 oz. Borax to 5 quarts water to 5 cu. ft manure.
6. Watered with can with 5 oz. Borax to 5 quarts water to 5 cu. ft manure, and later sprayed on the surface with 218 c.c. Creosote Oil Mixture, *i.e.* 1 gallon to 1 ton.

The treatment of No. 6 with borax was an attempt to drive the larvae up into the Creosote Oil Mixture.

Holes were drilled through the tubs at points 3 in., 6 in. and 12 in. from the surface, and tin tubes as used in a previous experiment (p. 69) were inserted to about 8 in. Temperatures were taken daily; and an average of the three holes calculated for each tub.

The untreated control showed a higher and quicker rise and a lower and more sudden fall than any of the treated tubs. A consideration of the other curves seems to indicate that treatment of manure with either Creosote Oil Mixture or with borax considerably delayed fermentation. So that such manure never gave temperature readings as high as the untreated and took longer to fall to the same level.

This experiment was started late in the season, when the manure possibly contained fewer eggs when collected and sufficient flies did not emerge from it to make the result decisive.

Though no flies emerged from tub 5 in this experiment, they did emerge from tub 6 of the first experiment, which was similarly treated. However, it may be noted that (1) the same quantity of very small flies emerged from the control and from No. 2 and about half that quantity from No. 3, but none from the remainder; (2) of the larger flies (*Scatophaga* and *M. domestica*) most (44) emerged from the control, whilst from each of Nos. 2 and 3, 3 specimens emerged; (3) there was no life in 4, 5, 6 (8 galls of Creosote Oil Mixture to 1 ton manure; borax; and borax plus 1 gall. Creosote Oil Mixture to 1 ton manure); (4) larvae were visible at any time in the control only; and no flies were caught over 4, 5 and 6, which would seem to show that the treatment of 4, 5 and 6 prohibited fly developement; (5) none of the larger flies emerged from these tubs in the spring of 1917.

The results of both these experiments may be summarised thus:

1. Surface sprayed manure gave higher temperatures than the unsprayed control, but though there was no sign of larval life on the surface at any time, fly developement was not prevented.
2. Larvae seem to be able to live just below the surface between the great heat below and the layer of Creosote Oil Mixture above. The temperature 1 inch below was, in one case, 41° C., which has been quoted as being the lethal temperature for larvae of *M. domestica* (Copeman, 1916).
3. Incremental treatment delays fermentation and consequently rise in temperature.

With the use of Creosote Oil Mixture in quantities up to 2 gallons to 1 ton of manure the temperature curve, though it does not rise so high, resembles that of the untreated manure; but larger quantities and borax, at the rate of 1 oz. borax to 1 quart of water to 1 cu. ft of manure altered the curve considerably. There was no rapid rise or fall as in the untreated heap—30° C. was hardly exceeded and 21° C. was the lowest temperature reached by manure so treated; whereas the untreated gave readings of 65° C. and 12° C.

No. 6 in experiment 2, treated with borax and creosote oil mixture gave still lower mean temperature.

4. Owing to possible uneven sampling of the manure in the first experiment and lateness of the season of the second, the minimum effective quantity of creosote oil mixture was not determined. But it should be noted that it seemed doubtful whether 1 gallon to 1 ton of manure would prove sufficient, whilst 4 gallons did prove effective.

5. Incremental treatment is superior to surface treatment.

6. Though the 6 tubs in experiment 2 were under observation until spring 1917 no *M. domestica* emerged from any of them after the winter.

EXPERIMENT TO ATTEMPT TO DETERMINE (1) THE DEPTH AT WHICH IT IS NECESSARY TO BURY MATERIAL INFESTED WITH FLY LARVAE, IN DIFFERENT SOILS, TO PREVENT THE ESCAPE OF THE ADULT, (2) THE EFFECT OF FILLING IN THE PITS LOOSELY OR OF RAMMING THE SOIL; AND (3) THE DISTANCE THROUGH WHICH THE ADULT FLIES ARE ABLE TO CLIMB WHEN EMERGING FROM PUPAE IN DIFFERENT SOILS, LOOSELY OR TIGHTLY PACKED.

In the *Military Manual of Elementary Hygiene*, 1912, two methods are given by which to dispose of excreta: (1) In the "Long and deep trench system" a trench 5 yards long × 16 inches wide × 3 feet deep is the allowance for 100 men; and "the contents of latrine trenches should be covered with a couple of inches of dry earth daily." (2) In the "Short and shallow system" the trench is made 1 foot deep and lasts 1 day, unless the contents is levelled down and the covering of earth is finely broken down, when it may be made to last longer." In paragraph 13, page 65, one is told that "so soon as the latrine-trenches have been filled in to within *six inches* of the ground level their use should be discontinued, earth thrown in, and turf or sods replaced."

As regards refuse it states that in bivouacs and camps of a temporary nature these receptacles (for disposal of refuse) may take the form of pits or holes, but where these are employed, the contents must be covered over with at least six inches of earth two or three times a day to prevent flies being attracted to them.

No instructions to vary the depth according to the nature of the soil are given. A couple of inches of dry earth thrown over the excrement would probably be insufficient to prevent the material becoming infested with flies' eggs; and six inches has been proved too little to prevent the escape of any flies developing (see Graham-Smith, 1916, p. 503).

Henri Fabre found that *Sarcophaga carnaria* could traverse a column of sand six inches high in 15 minutes; and in an experiment, in which he placed lots of 15 pupae of *Calliphora* at the bottom of large glass tubes, which were then filled with different quantities of sand, found that from those pupae covered with

6 cm. (2·34″)	of sand	14	out of 15	flies	reached	the surface
12 cm. (4·68″)	,,	4	,,	,,	,,	,,
20 cm. (7·8″)	,,	2	,,	,,	,,	,,
60 cm. (23·4″)	,,	1	,,	,,	,,	,,

Hewitt (1915) found pupae of *M. domestica*, from which flies had successfully emerged, 24 inches below the ground in light soil.

Graham-Smith (1916) made the following observations on burial of infested material: (1) "On July 7th a large piece of sheep's lung containing some eggs and very small larvae was buried to a depth of 1½ feet, and the earth well packed down. The earth was further trodden down on July 9th. On July 12th the material was exhumed and numerous large, apparently healthy, larvae were found in it." (2) "On September 4th the bodies of six guinea-pigs were exposed. On the same day one of the carcasses with eggs in the mouth and on the hair was buried to a depth of one foot in an earthenware pipe sunk vertically in the ground. A little earth was placed above the carcass and packed down tightly, and the process repeated till the pipe was full. The top of the pipe was sealed with an earthenware saucer. The other carcasses containing larvae of various sizes were similarly buried on September 8th, 10th, 11th and 14th. On September 26th full fed larvae and pupae were noticed just below and on the surface of the earth in all the pipes. Blow-flies began to emerge simultaneously from all the pipes on October 17th, and large numbers were caught up to October 29th, and smaller numbers up to November 15th. These observations show that larvae emerge from eggs and thrive in buried carcasses, and that they are able to make their way to within a short distance of the surface where they pupate. And that the burial of a carcass does not prevent flies emerging from eggs already laid, but only limits the production of flies by preventing later batches of eggs from being deposited."

The greatest depth tested by Fabre and by Graham-Smith was 23·4 inches and 18 inches respectively.

During May 1917, a hole *ABCD* (Fig. 6) about 4 ft × 4 ft × 4 ft 6 in. deep with an approach trench *GCEF* was dug in light loam soil. The floor was covered with sand to a depth of two inches to enable the concrete to bind. A two inch layer of concrete was spread over the sand and six roughened slates were sunk into it; and a land drainage pipe one foot long and six inches in diameter was then placed upright on each of the slates on to which it was carefully cemented. When the cement had set the hole was filled in with earth to the level of the top of the pipes. A layer of sand was then spread round the mouths of the pipes and a second lot of pipes was cemented on to the first lot with a fresh layer of cement, which was sloped up to the pipe to ensure covering the joint completely. This process was continued until there were four tiers of pipes, *i.e.* until there were six holes six inches in diameter and four feet deep, from which no larvae could escape save upwards. The pipes were then numbered as shown in the diagram.

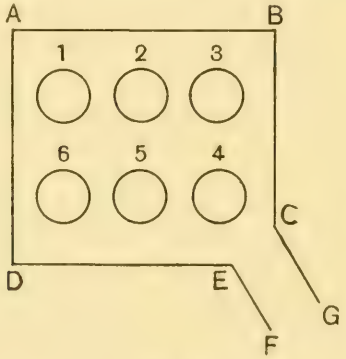


Fig. 6.

Many *C. erythrocephala* females were placed in a large muslin cage (Graham-Smith, 1914, Pl. XIX, fig. 3) with bodies of four guinea-pigs and of one large rabbit, which had been dead for several days, in order that they might thoroughly infest the carcasses with their eggs.

On May 2nd the body of a dead guinea-pig, which was swarming with larvae of *Calliphora*, was dropped into each of holes 1 and 2, which were then filled in with loam—the soil in 1 being loosely packed, but that in 2 tightly. On May 4th similarly infested remains were placed in 3, 4, 5 and 6; the first two being filled with sand and the last two with clay. Nos. 3 and 5 were loosely filled, but 4 and 6 tightly packed. The contents of 2, 4 and 6 were packed by filling them by degrees and ramming each lot of soil down with a long wooden pole.

A trap to catch any flies which might emerge was constructed over each pipe. A small piece of wood, with a half-inch hole in the middle, and to which muslin was tacked (Fig. 5), was supported on four wires, which were pushed firmly into the soil round each pipe. The edges of the muslin were covered with soil, and a balloon trap was placed over the hole in the wooden top.

Flies emerged from all the pipes between July 1st and August 28th, 1917. A total of 2516 was caught and 9 species represented (see Table II).

Between December 29th, 1917, and January 2nd, 1918, the earth round the pipes was dug out, and sections were taken from each pipe at levels of 1, 8, 12, 18, 24, 30, 36, 42 and 48 inches, in the following way. The blade of a hack-saw, which had been marked at distances of 1 and 3 inches from one end, was pushed down the inside of a pipe until the inch mark was level with the top of the pipe. The soil was then carefully removed to that level; the blade being worked round to ensure not going too deep. The same procedure was used to obtain the 3 inch sections. The 8, 18, 30 and 42 inch levels were determined by careful measurements outside the pipes: a hole being made at the point with a cold chisel. The flat blade of a hack-saw was then thrust in horizontally, through the hole made, and the earth removed to that level. The 12, 24, 36 and 48 inch levels occurred at the cement joints, which were opened by means of a cold chisel. By thrusting in a piece of slate, it was then possible to remove the rest of the pipe and push from it the remaining section of soil.

Each section, as extracted from the pipe, was placed in a biscuit tin and marked; dried separately and passed through a 3 mm. sieve over white paper: pupae and remains of flies being extracted. The results are shown in Table III.

Owing to unavoidable absence from Cambridge the traps were not visited every day. On August 5th, after 7 days continuous rain, the muslin was found to have worn through round the rims of the pipes. The rents were repaired immediately, but this occurred between the 28th and 35th days after that on which the flies started to emerge; and the flies continued to appear in the traps up to the 59th day. A certain number of flies, therefore, may have escaped during the 7 days above mentioned, which may account for the discrepancy between the number of pupae found and flies caught in pipes 2 and 3.

A few pupae were noticed outside in the soil surrounding the pipes, which indicates that a certain number of larvae probably made their way completely through the 4 feet of soil and pupated outside.

The animal matter at the bottom of all the pipes except 2 and 6 was entirely consumed, only the bones being left. In 6 there remained a little dry skin and hair attached to some of the bones, but in 2 the greater part of the animal still remained, forming a moist evil smelling mass of hair and rotten flesh. This would suggest that the larvae in pipe 2 died for some reason, which would account for the comparatively low numbers of pupae found and flies caught from it.

Owing to unavoidable delay (4 months) in opening the pipes, it is possible that a number of pupa cases and bodies of adult flies had rotted beyond recognition. Only five bodies of adult flies were found and they were much decayed. Three of these bodies were found in the loose clay, being between the 1 inch and 3 inch levels, and probably had died of exhaustion, whilst of the other two, one was found between the 30 and 36 inch levels, and the other between the 40 and 48 inch levels. The fifth was found in the rammed clay between 42 and 36 inch levels.

Some of the pupae which were found at the lower levels were ill-formed, but those in pipes 8, 2 and 3 were normal healthy ones. Only five were found to have been parasitised, though some of those which had disintegrated may have been so.

From this experiment two facts seem evident, namely, (1) flies are able to develope from larvae which have been buried as deep as 4 feet, and that it is, therefore, useless to bury larvae-infected material, even at that depth, to prevent fly developement; and (2) the majority of larvae (90 per cent. in this experiment) make their way up to within a foot of the surface of the soil before pupating.

Table II.

Showing numbers of flies which emerged between July 1*st and August* 28*th,* 1917, *though their larvae had been buried within food material four feet below the surface of ground.*

	Loam				Sand				Clay (dryish)			
	Loose 1		Rammed 2		Loose 3		Rammed 4		Loose 5		Rammed 6	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Calliphora erythrocephala	104	106	5	5	161	127	266	407	348	341	91	102
,, *vomitoria*	10	21	2	0	1	5	18	44	57	93	—	1
Lucilia caesar	1	1	—	—	—	—	4	7	19	29	5	4
,, *sericata*	1	2	—	—	—	—	6	7	38	26	6	—
Hydrotaea dentipes	—	—	—	—	31	4	—	—	—	—	—	—
Muscina stabulans	—	—	—	—	—	—	—	—	—	—	—	6
,, *pabulorum*	—	—	—	—	—	—	—	—	—	1	—	—
Small Anthomyidae	—	—	—	—	—	—	—	1	—	—	—	—
?	—	—	—	—	—	—	—	—	—	—	1	1
Totals (sexes)	116	130	7	5	193	136	294	466	462	490	103	114
Total flies	246		12		329		760		952		217	
	2516											

TABLE III.

Showing pupae and remains of flies found at different levels; and the per cent. of larvae which had climbed to within one foot of the surface before pupating. + = remains of a fly.

	Loam				Sand				Clay					
	1 Loose		2 Rammed		3 Loose		4 Rammed		5 Loose		6 Rammed		Section totals	
From surface														
to 1″ below	4	113	0	18	0	650	6	541	5	706	51	144	66	
1″– 3″	50	i.e.	0	i.e.	1	i.e.	445	i.e.	111	i.e.	13	i.e.	620	2171
3″– 8″	45	88	0	86	560	95	81	97	541	96	69	92	1295	i.e. 95 %
8″–12″	14	%	18	%	89	%	9	%	49	%	11	%	190	
12″–18″	5 +		0		22		5		16		8		56	
18″–24″	0		0		3		6		10		2		21	
24″–30″	3		1		3		3		3		1		14	
30″–36″	2		1		4		0		+		0		7	
36″–42″	3		1		2		0		1		1		8	
42″–48″	1		0		3		3		+		0		8	
Total pupae	127		21		687		558		736		156		2285	

SUMMARY OF INVESTIGATIONS.

During the winters of 1915–1916 and 1916–1917 manure heaps and other likely places were searched for dipterous larvae and pupae. During the summer (1916 and 1917) observations were made on fly distribution in town and in country and various experiments were carried out to investigate the temperature conditions in loosely packed and tightly packed manure heaps, and the influence on those conditions and on fly developement of applications of creosote oil mixture and of borax in various quantities; to determine the amount of creosote oil mixture necessary to apply to prevent fly developement and the best way to apply it; to determine whether horse manure which had ceased to ferment was still attractive to adult flies or could provide nourishment for their larvae; to find out at what depth fly-larvae-infested material may safely be buried in different soils, loose or rammed, to ensure no flies emerging, and to what height the larvae would climb in those soils before pupating.

The results may be summarised thus:

1. Thirty-nine species of fly were bred from larvae or pupae found in natural situations during the winter. Of these 31 are additional to Dr Graham-Smith's (1916) list.

2. Pupae of *Musca domestica* were found but the adults were not reared; even though, in one experiment, lots of 1 cwt. of horse manure were kept under observation in barrels from autumn until the following spring.

3. The distribution of dipterous larvae in a manure heap in winter, at any rate in the Eastern Counties, is extremely local and, therefore, calculations based upon the number of larvae or pupae per pound of manure are futile.

4. Usually there seemed to be little preference shown by the larvae for any particular part of the heap, but in a few cases they seemed to select the portions which received least light.

5. During the summer and autumn *M. domestica* was found in largest numbers, in town and in the country, in the neighbourhood of horse manure—in the latter case in and about farmyards and buildings, and in the warm kitchens of farm-houses. But the numbers were found to decrease markedly when isolated houses in the country or manure heaps far from buildings were examined.

6. In farmyards and manure heaps near buildings in the country such genera as *Stomoxys*, *Scatophaga*, *Borborus* and *Limosina* predominated.

7. *M. domestica* was observed alive in town as late as December 2nd outside and December 9th inside; but one was caught in a house in Grantchester during the last week in December, 1917. Probably those seen in 1916 lingered sometime longer, but these places were not revisited in that year.

8. Flies were bred during summer from material used in summer investigations as follows: human faeces—*Hydrotaea*, *Scatophaga*, *Sarcophaga*, *Muscina stabulans* and small *Anthomyidae*; pig manure—*Mydaea*, *Scatophaga*, *Sarcophaga* and small *Anthomyidae*; cow manure—*Morellia 'hortoum*, *Eristalis*, *Scatophaga*, *Limosina*, *Psycodidae* and *Borboridae*; horse manure—*Stomoxys*, *Borboridae*, *Limosina*, *Psychodidae* and small *Anthomyidae*; small carcasses—*Hydrotaea* and *Calliphora*.

For flies bred from larvae and pupae found in various manures during winter see Table I.

9. Horse manure, which has ceased to ferment and is cold, has no attraction for the adults of *M. domestica* nor nourishment for its larvae, though it still attracts small species such as *Limosina*, *Psychodidae* and *Borboridae*; and though larvae of certain species of fly have been found in it throughout winter.

10. 99·5 per cent. of the flies bred from horse manure, made in a town stable during 24 hours in the autumn, were *M. domestica*, which emerged during 14 days, commencing on the 12th day.

11. Male *M. domestica*, as a whole, started emerging sooner than the females.

12. The temperature in a loosely packed heap of horse manure rises

higher and falls sooner and lower than that of a tightly packed one. The maximum temperature in a loosely packed heap is reached about the third day.

13. The deeper portions of a tightly packed heap remain at a higher temperature for a longer time and then fall suddenly.

14. Creosote oil mixture should be sprayed "*Incrementally*" and not merely on the surface.

15. It is doubtful whether 1 gallon to the ton of manure is sufficient to prevent flies from emerging. Four gallons proved enough, but it was not possible to carry out sufficient experiments to determine the precise minimum quantity necessary to prohibit developement of flies.

16. Incremental applications of creosote oil mixture and of borax lower the general temperature of the heap. The temperature never rises as high and takes much longer to fall as low. This is probably due to fermentation being delayed.

17. If a heap is sprayed on the surface with creosote oil mixture, *M. domestica* larvae are able to live between the sprayed surface and the intense heat below. The temperature 1 inch below the surface of the manure, when that of the heap is near its maximum, is about 41° C.—a temperature of which Howlett wrote "It is improbable that they (larvae) could live long at anything over 41° C. (about 106° F.)"—see Copeman (1916).

18. It is useless to bury larvae-infested material at a depth of 4 feet in clay, loam or sand, whether loose or rammed down, as the majority of flies will emerge.

19. About 90 per cent. of the larvae, so buried, climbed to within 1 foot of the surface before pupating.

20. The following parasites were bred—from two pupae of *Hydrotaea dentipes* two *Ichneumons* (*Atrodectes tenebricosus* Grav. ♀, *A. exilis* Hal. ♂), from a third pupa of *H. dentipes* a *Figitid*; from pupa of *Lonchaea vaginalis* or *R. radicum* an *Ichneumon*; from two Calliphora-like pupae one and two *Figitids* respectively; and from three pupae of *Eristalis tenax* 72 (10♀, 62♂), 24 and 8 (5♂, 3♀), *Proctotrypids—Diapria conica*, Fabre, were extracted dead.

REFERENCES.

BISHOPP, F. C., DOVE, W. E. and PARMAN, D. C. (1915). Notes on certain points of economic importance in the biology of the House-fly. *Journ. Econom. Entomol.* VIII, pp. 54–71.

COPEMAN, S. M. (1913). Hibernation of House-Flies. *Reports to the Local Government Board on Public Health and Medical Subjects*, New Series, No. 85, pp. 14–19.

—— (1916). Prevention of Fly-Breeding in Horse Manure. *The Lancet*, June 10th, 1916.

Copeman, S. M. and Austen, E. E. (1914). Do House-flies hibernate? *Reports to the Local Government Board on Public Health and Medical Subjects*, New Series, No. 102, pp. 6–26.

Dove, W. E. (1916). Some notes concerning over wintering of the House-Fly, *Musca domestica*, at Dallas, Texas. *Journ. Econom. Entomol.* ix, pp. 528–539.

Fabre, J. H. *Souvenirs Entomologiques*, 19e Serie, Delgrave, Paris.

Forman, F. W. and Graham-Smith, G. S. (1917). Investigations on Prevention of Nuisances arising from Flies and Putrefaction. *Journ. Hygiene*, xvi, 2, pp. 119–226.

Graham-Smith, G. S. (1914). *Flies in Relation to Disease. Non-Blood-Sucking Flies.* Cambridge University Press.

—— (1916). Observations on the Habits and Parasites of Common Flies. *Parasitology*, viii, pp. 440–544.

Griffith, A. (1908). Life-History of House-flies. *Pub. Health*, xxi, pp. 122–127.

Hermes, W. B. (1911). The house-fly in its relation to public Health. *University of California publications, Bull.* Nov. 215, pp. 513–548.

Hewitt, C. G. (1910). The House-Fly. *A Study of its Structure, Development, Bionomics and Economy.* Biological Series, No. 1. Manchester University Press.

—— (1912). *Fannia* (*Homalomyia*) *canicularis* Linn. and *F. scalaris* Fab. An account of the Bionomics of the Larvae and their relation to Myiasis of the intestinal and Urinary Tracts. *Parasitology*, v, pp. 161–174.

—— (1914). Further Observations on the Breeding Habits and Control of the House-fly, *M. domestica. Journ. Econom. Entomol.* viii, 3.

—— (1914). Observations on the feeding Habits of the Stable Fly. *Transactions of the R. S. Canada*, Series iii, vii.

—— (1915). Pupation and Over wintering of the House-fly. *Canadian Ent.* xlvii, No. 3, pp. 73–78.

Howard, L. O. (1911). House Flies. *U.S. Dep. Agri. Farmers Bull.* No. 459.

—— (1912). *The House Fly, Disease Carrier. An Account of its dangerous activities and of the means of destroying it.* John Murray, London.

Kieffer, l'Abbe J. J. et le Rev. T. A. Marshall (1907). Les Proctotrypidae, Pt 2, in André, *Species des Hyménoptères*, Tome x.

Kisliuk, M. (1917). Some Winter Observations of Muscid Flies. *Ohio Journ. Sci. Columbus*, xvii, No. 8 (*Rev. App. Ent.* v, Ser. B, Sept. 1917).

McDonnell, R. P. and Eastwood, T. (1917). A Note on the Mode of existence of Flies during winter. *Journ. R.A.M.C. London*, xxix, 1.

Newstead, R. (1907). *Preliminary Report on the Habits, Life Cycle and Breeding places of the Common House-Fly* (*Musca domestica, Linn.*), *as observed in the city of Liverpool, with suggestions as to the best means of checking its increase.* C. Tinling and Co., Liverpool.

—— (1909). *Second Interim Report on the House-Fly, as observed in the City of Liverpool.* C. Tinling and Co., Liverpool.

Portchinsky, J. A. (1913). Review in *Review of Applied Entomology*, 1, B, pp. 149–152.

Skiner, H. (1913). How does the House-Fly pass the Winter? *Entom. News, Philadelphia*, xxiv, pp. 303–304.

Williston, S. W. (1908). *Manual of North American Diptera.* James F. Hathaway, New Haven.

VOLUME VI DECEMBER, 1919 NOS. 2 AND 3

A PHYTOPHTHORA ROT OF PEARS AND APPLES.

BY H. WORMALD, D.SC. (LOND.), A.R.C.SC.

(*Mycological Department, South-Eastern Agricultural College, Wye, Kent.*)

(With 2 Text-figures and Plate III.)

THE ROT ON PEARS.

IN September, 1912, two pears affected with a soft rot were received at Wye from a garden in Hertfordshire. The sender stated that the disease started at the stalk end of the pears and caused them to fall before they reached maturity. The appearance at the surface of the affected pears was different from that produced by the rots commonly met with, in that there were present numerous glistening points which were evidently highly refractive granules, bearing a striking resemblance to hoar-frost. On microscopic examination these particles proved to be clusters of sporangia borne on short unbranched sporangiophores projecting in tufts through the ruptured epidermis, each sporangiophore bearing a terminal sporangium.

The rather coarse non-septate mycelium present in the discoloured tissues, and the type of sporangia found on the surface were typical of those of the Peronosporaceae, and as no record could be found of the occurrence of a member of this family on pears in this country further investigation was made.

Reference to foreign literature revealed the fact that a similar disease had been observed on apples and pears on the Continent, and on apples in America. The earliest record appears to be that of Osterwalder(4) who in the summer of 1904 found numerous fallen fruit under cordon apple trees in Switzerland. When these apples were placed in a moist chamber numerous oospores developed; on immersing the apples in water sporangia were also formed and Osterwalder was able to identify the fungus as *Phytophthora Cactorum* (Lebert et Cohn) Schröter = *P. omnivora* de Bary. In 1908 Marchal(3) described the same fungus as producing a rot of pears in Belgium, the disease causing the fruit to fall prematurely. Two years later a similar rot, also on pears, was recorded by Bubák(1) as occurring in Bohemia; from his descriptions and figures there is reason for assuming that the disease he observed is identical with that of the Hertfordshire specimens. The clusters of sporangia, which he observed on the pears, he refers to as "stark lichtbrechen Körnchen, die habituell kleinen Zuckerkristallen ähnlich waren." About the same time Unamuno(12) found *Phytophthora Cactorum* associated with a disease of pears and cherries in Spain. In 1912 Osterwalder(5, 6) again refers to the occurrence of this fungus on apple trees in Switzerland, a die-back of the shoots being observed in this case.

While the outbreaks mentioned in the present article were under investigation two other references to fruit rots caused by a *Phytophthora* have appeared. Schoevers(11) in 1915 recorded a rot of pears in Holland attributed to *P. omnivora*, and in 1916 Whetzel and Rosenbaum(13) mention a *Phytophthora* rot of apples as occurring in America. The latter isolated *P. Cactorum* from the diseased fruit and were able to reproduce the disease on apples on the tree by inoculations with mycelium from pure cultures.

As the disease appeared to be of some economic interest and one on which no work had been done in this country more specimens were obtained, and these showed the same general features as those previously examined. The letter accompanying them stated that "the smaller variety is Fondante d'Automne, the larger one Doyenne du Comice; all the pears of the former one started to go at the base and fell within three days, now the latter pear has just commenced to fall in exactly the same way."

On keeping the affected pears in a closed glass vessel the sporangia were gradually replaced by sexual organs and oospores, the latter 22–30μ in diameter, with smooth walls; the sexual organs were of the *Phytophthora Cactorum* type or genus *Nozemia* of Pethybridge(7). It was highly probable therefore that the sporangia and the oospores belonged to one and the same organism and inoculation and cultural experiments confirmed this supposition.

Inoculation Experiment 1. Three pears were wounded by making cuts through the skin, and sporangia from an infected pear were placed on the wounds; at the end of 20 days one of the pears had produced sporangia while on the other two only sexual organs were found. A pear which had been inoculated at the same time by placing sporangia in a drop of water in the hollow at the stalk end, without injury, showed no change after 20 days.

The fungus was then grown in pure cultures. No difficulty was experienced in isolating it, for by transferring, on the point of a sterile needle, a few of the highly refractive granules from a diseased pear to agar, mycelium grew out and developed numerous oospores, no other organisms appearing. The fungus grew readily on such culture media as prune agar, celery agar, maize meal agar and French bean agar, and numerous oospores developed, but no sporangia were observed on these media; on nutrient starch jelly there was feeble growth and no reproductive bodies were found.

Inoculation Experiment 2. The *Phytophthora* was cultivated in the laboratory during the winter, and in the following summer two pears were inoculated with mycelium from a plate culture. Within seven days both pears were discoloured over an area extending 3·5 cm. from the point of inoculation; one showed many sporangia and sexual organs also, the other bore sexual organs only.

In order to prove conclusively the connection between the sporangia and the oospores the following cultural experiment was carried out. From one of the pears sporangia were taken and diffused in a little sterile distilled water and drops transferred with a platinum wire loop to the surface of prune agar in a Petri dish. Three of these drops, examined under a low power of the microscope, were found to contain but one sporangium each; these three were marked on the bottom of the dish, with a ring of ink round each, and kept under observation. Within 24 hours two of them had germinated and produced a number of germ tubes; in one case the germ tubes formed a diverging tuft at the non-papillate end of the sporangium, while in the other they were scattered and not localized to any particular part of the surface. The longest germ tube was 0·9 mm. in length. The two sporelings were transferred to other plates and within five days from the isolation of the sporangia, which under these conditions germinated as conidia, both had developed sexual organs similar to those observed on the pears, thus showing that the two types of reproductive bodies belong to the same fungus.

Inoculation Experiment 3. Two pears were inoculated by making a cut through the skin and placing in the wound mycelium from one of the sporelings. Within 10 days both pears had become infected and the fungus had developed the glistening particles characteristic of the disease on pears. The particles were most numerous towards the edge of the affected area, and again each was found to be a cluster of sporangia; no superficial sterile mycelium was present at such places. On the other hand, in the immediate neighbourhood of the point of inoculation mycelium was seen on the surface as a white felt; here the sporangia were fewer in number and sexual organs were present. The affected internal tissues were found to be permeated with the non-septate mycelium. A small portion of a section, made with a sterilized razor through the infected flesh of one of the pears at 0·5 cm. below the surface, was placed on agar and gave rise to a culture similar, in general appearance and in the production of sexual organs, to those cultures obtained from sporangia.

Inoculation Experiment 4. On August 9, 1913, an experiment was carried out on pears growing in the open. Five were inoculated by making a wound through the skin and inserting mycelium from a pure culture growing on agar. Two pears were similarly wounded but sterile agar was placed in the wounds. A fortnight later one of the pears inoculated with mycelium was found on the ground and two others fell at a touch while under examination; the rest, including the controls, remained on the tree uninfected until ripe.

The pear found on the ground had been attacked by another fungus, for on keeping it in a damp chamber no fructifications appeared and a particle of the flesh placed on agar gave rise to growth unlike that of the *Phytophthora*. The other two infected pears, however, produced numerous sporangia on being kept for a few days in a damp chamber.

Two of the five pears inoculated with mycelium had therefore become affected with the *Phytophthora* rot.

Inoculation Experiment 5. In the following year an experiment was carried out on young pear trees growing in pots in the greenhouse. On September 10 eight pears were inoculated (four of each of the varieties Fondante d'Automne and Doyenne du Comice) with mycelium from a pure culture as in the preceding experiment, and on the opposite side of each pear a control wound (not inoculated) was made. At the end of six days five of the pears showed a blackened area 1·5 cm. in diameter round the inoculated wound and in a fortnight from the beginning of the experiment the rot had made distinct progress in all, half the surface in six of the pears being affected and about one quarter of the surface in the other two. On the control side of each no rot occurred at the wound except in one case in which a soft rot caused by a *Botrytis* made its appearance.

Under the conditions which obtained in the greenhouse no sporangia were seen at this stage, the atmosphere probably being too dry, so three of the infected pears (including the one with *Botrytis*) were cut off and placed in damp chambers; *Phytophthora* sporangia developed, on the side inoculated, in each case within a few days. Of the five remaining, one was found on the ground on September 29, and two others, which were discoloured over the whole surface with the exception of a small green patch near the eye end, fell at a touch on the same day; the other two hung on the tree until October 15, by which time they were soft and discoloured over the whole surface, the stalks being brown and withered. Again no reproductive bodies were to be found on these pears while they remained in the greenhouse, but on being transferred to a damp chamber sporangia readily appeared within a few days.

About six weeks after the inoculations were made one of the pears was cut across and examined for the presence of mycelium in the tissues. Non-septate hyphae were found extending to the centre of the pear, invading the cavities of the core and forming a covering round the seeds; strands of mycelium were seen even within the seeds themselves. A small portion of the testa with the adhering mycelium was removed from one seed and after washing in several changes of sterilized distilled water it was transferred to agar in a test tube; a typical pure culture of the *Phytophthora* resulted, sexual organs developing within five days.

Inoculation Experiment 6. From one of the pears used in the last experiment sporangia were transferred to a little distilled water on a glass slide; after a few hours numerous zoospores were set free so drops containing motile zoospores were placed on the stalk end of two pears on a tree in the greenhouse on September 29, while the pears were still quite hard and not nearly ripe. One of the pears was found detached on October 2 although no signs of rot were evident. The second fell on October 9 and showed a discoloration extending from the stalk end for about 1 cm. down one side; the pear was placed in a damp chamber and within three days the rot had extended all round the stalk end to a distance of from 1·3 to 2·2 cm. and sporangia were present.

As the atmosphere in the greenhouse was rather dry the inoculations were made in the evening and the two pears were enclosed in transparent water-proof bags containing a little absorbent cotton wool soaked with distilled water; these precautions were adopted to prevent the rapid evaporation of the drops of water containing the zoospores.

The result suggests that the zoospores are able in certain circumstances to cause infection through the uninjured skin, particularly in a moist atmosphere. On repeating the experiment the following year on eleven pears, not enclosed in bags, negative results were obtained in all cases.

The Sporangia and their Mode of Germination. As found on the affected pears the sporangia were mostly elliptical or citriform; the smaller ones were almost spherical, but others were elongate with a slight constriction near the middle. Their dimensions were in general $35\text{-}65\mu \times 22\text{–}35\mu$, the papillae being $4\text{–}6\mu$ in length, but occasionally sporangia $70\text{–}80\mu$ in length were observed.

The sporangiophores were $20\text{–}40\mu$ in length and emerged through the epidermis in small tufts; each sporangiophore bore a single sporangium terminally. In certain coverglass cultures on films of prune agar, however, hyphae were produced which developed sporangia sympodially in the manner generally typical of the genus *Phytophthora*, series of 3, 4 and 5 sporangia respectively being formed in this way; no localized swellings such as are characteristic of the sporangiophores of *P. infestans* were seen on these sporangiferous hyphae.

The rich development of sporangia on pears afforded a good opportunity of studying their mode of germination. On agar they always germinated directly by giving rise to several germ tubes. In hanging drops of tap water they germinated in one of three ways, viz.

(1) Some produced branched germ tubes often swollen at the apex, with a tendency for the protoplasm to become aggregated into the swollen ends of the branches.

(2) Others gave rise to zoospores which were liberated into the water.

(3) In a few cases the protoplasm became rounded off to form zoospores which however did not escape into the water but germinated, by developing germ tubes, within the sporangium.

In distilled water the sporangia sometimes germinated by producing germ tubes directly but usually zoospores were formed, and generally numerous zoospores could readily be obtained by transferring sporangia from an infected pear to a drop of distilled water on a slide. The number of zoospores produced by a sporangium is about 30 or 40; four sporangia of which the zoospores were counted as they emerged gave rise respectively to 31, 43, 31 and 38 zoospores.

The time taken for the sporangia to become emptied was ascertained in a few instances by means of a stop-watch. Two sporangia, in which the number of zoospores was not determined, were emptied in 33 and 36 seconds respectively; in two others 31 zoospores took 31 seconds while 43 required 51 seconds. In some cases the liberation of zoospores was more irregular, thus from one sporangium 18 escaped in 20 seconds, after which 12 others, emerging more slowly, required 70 seconds, and there was still one zoospore left which remained there for some minutes. From another sporangium 25 zoospores escaped in 75 seconds; $2\frac{3}{4}$ minutes later two others emerged, leaving 11 which were still within the sporangium after 15 minutes.

The zoospores which escape first (to about 10 in number) are difficult to count for they are expelled in an almost continuous stream and cling together, surrounded by a vesicle, just outside the mouth of the sporangium, for about a second before suddenly dispersing (Fig. 1). The vesicle is derived from the hyaline plug forming the papilla; this is pushed out as a spherical transparent body which rapidly increases in size as the zoospores rush in. When its diameter is about equal to the

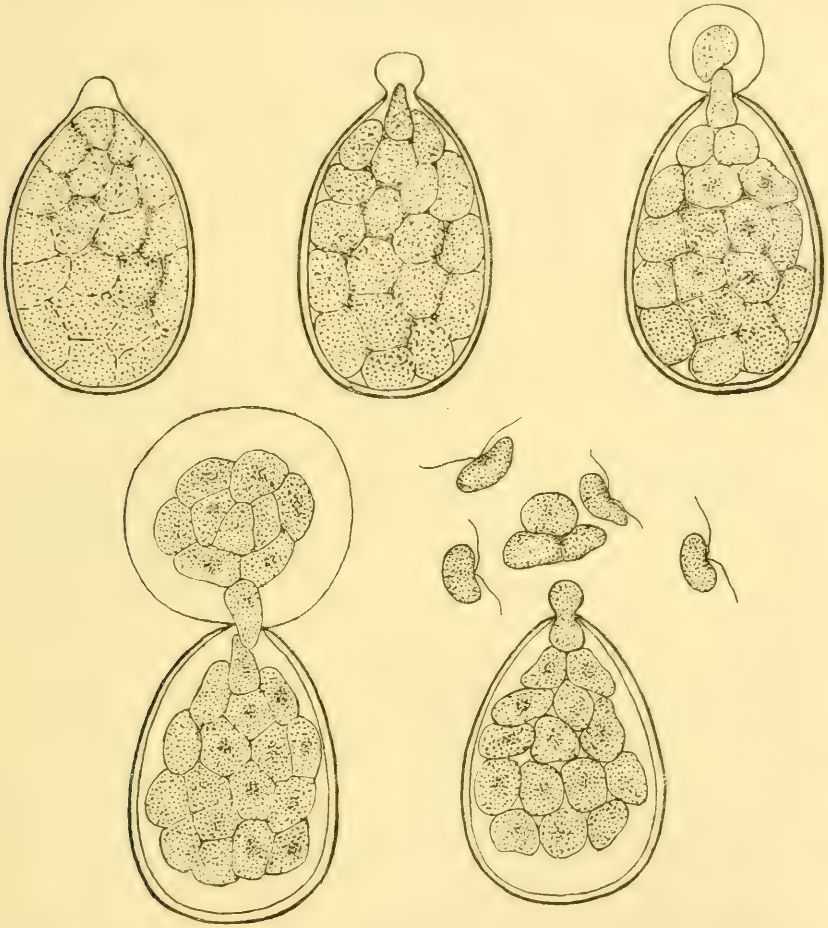


Fig. 1. Zoospores escaping from a sporangium, with the formation of a vesicle.

length of the sporangium the vesicle suddenly becomes ruptured and disappears from view, the enclosed zoospores dispersing immediately. The rest of the zoospores come out singly in rapid succession and have to squeeze their way through the opening, becoming hour-glass shaped when half-way through. If one should fail to get out with the main stream it swims about frantically inside the now almost empty sporangium; one that was so left behind escaped eventually but took two or three minutes to force itself through the mouth of the sporangium. On reaching the exterior the zoospores are at first somewhat irregular in shape for they appear to undergo temporary deformity during the passage through the narrow aperture, and often make a slight pause, just outside the mouth of the sporangium, in order to resume their normal form before swimming away.

The size of the zoospores was usually not easy to determine owing to the rapid movements but occasionally approximate measurements were possible and the dimensions found to be about $12 \times 9 \mu$. The zoospores are pyriform to reniform with two cilia inserted within the sinus.

When in motion the zoospore revolves round its longitudinal axis. The posterior cilium projects backwards like a flexible bristle, becoming inclined with each change of direction of the body of the zoospore. The anterior cilium is very rarely seen but a glimpse of it may be obtained when the zoospore pauses for a moment. Even then its appearance is only momentary and at first it was thought possible that it was the posterior cilium brought round anteriorily. Later, however, both were occasionally seen at the same time, one directed forward, the other backward. It would seem that the anterior cilium is the organ of locomotion for its invisibility when the organism is in motion doubtless indicates that it is in rapid vibration.

In those cases where the zoospores emerge slowly from the sporangium cilia can be seen while they are still inside the sporangium. It is probably the anterior cilia which are visible in this case for they are pointed towards the mouth of the sporangium; again when a zoospore is about half-way through the aperture its anterior cilium may again be seen turned over to one side, then as the zoospore becomes free the other cilium is seen trailing behind through the opening (Fig. 2).

Sometimes a zoospore was seen having a posterior attenuated "tail" of protoplasm. On one occasion two zoospores were found attached to each other by a protoplasmic strand; in such a case co-ordinated movement seemed to be absent for they swayed from side to side without making any definite directive movement. In another instance two zoospores appeared to be attached by their cilia for a delicate fibril was seen to be connecting them; by their frantic efforts this was soon broken and they disappeared in opposite directions.

Frequently fragments of protoplasm remained just outside the mouth of the sporangium after the zoospores had swum away; these became rounded off and showed no signs of movement. The zoospores after swimming about for some time lost their motility, assumed a spherical form and began to germinate, each producing a single germ tube.

The vesicle which is produced when the zoospores are liberated from a sporangium is transparent and only just visible during the short time taken in its expansion; it is produced so rapidly and is so very evanescent, disappearing from view while more than half the zoospores are still within the sporangium, that it may easily escape notice, and is probably of more general occurrence than is usually supposed to be the case. The observations here recorded were made in the summer of 1913. In the same year Dastur (2) recorded and figured the vesicle for *Phytophthora parasitica*; Rosenbaum (10) in 1917 recorded having observed it in *P. Cactorum*, *P. Arecae* and *P. parasitica* and quite recently Pethybridge and Lafferty (8) have observed it in *P. cryptogea*. On the other hand Robinson (9) states that he has never observed it in the *Phytophthora* which he found associated with a Wilt Disease of Asters and assumes that the absence of the vesicle is a characteristic of the genus distinguishing it from *Pythium*.

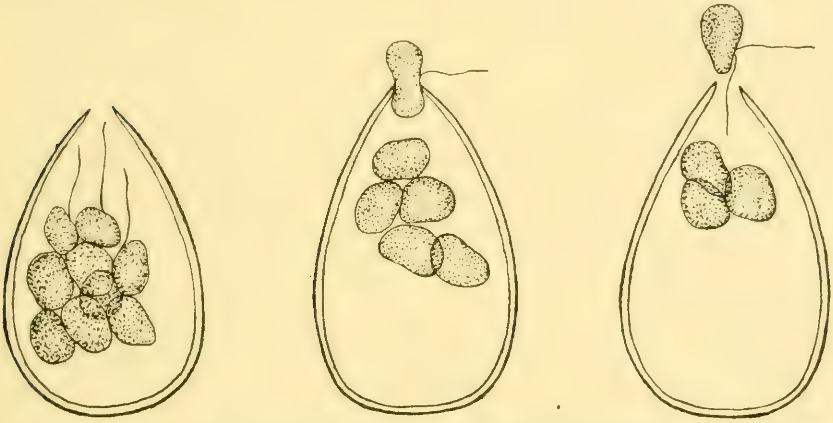


Fig. 2. A sporangium from which the zoospores emerged slowly; the orientation of the cilia was seen under those conditions.

THE ROT ON APPLES.

In the summer of 1915 two apples affected with a soft rot were received from Surrey, the diseased areas showing, where the skin was ruptured and turned back, a white "bloom" which proved to be mycelium; a few sporangia of the *Phytophthora* type were obtained from one of the apples. Later other specimens were obtained from the same source; they were all of one variety of apple, viz. Lane's Prince Albert. The majority of these again showed the white film of mycelium where the flesh was exposed. One of them had no trace of any fungus on the surface although nearly half the apple was soft and brown; the diseased tissues however contained rather coarse, guttulate, non-septate hyphae, and particles of the flesh, cut out with a sterilized razor and placed on agar developed into cultures similar to those obtained from the *Phytophthora* on pears.

The white "bloom" was seen only on those apples where the skin had become torn and had rolled back exposing the flesh underneath; this condition obtained in most of the apples examined (see Plate III, fig. 3). In those where the skin was intact the mycelium was either not apparent at the surface or it issued through the skin as small tufts of hyphae which were quite barren, neither sporangia nor sexual organs being found on them.

Sporangia occurred far less frequently on these apples than on pears infected with the disease; of the 14 affected apples examined sporangia were found on four only at the time they were received. Osterwalder(4) found that such apples could be induced to develop *Phytophthora* sporangia freely by immersion in water, so one of the apples on which no sporangia could be found was immersed in a beaker of water which was then covered with a bell-jar. Within 24 hours a white weft of mycelium had grown out into the water; on placing a little of this mycelium on a slide numerous sporangia were seen and on adding a little distilled water numerous zoospores were liberated within two hours.

In 1917 two apples showing a similar rot, no reproductive bodies being present, were received from Sussex; the tissues however were permeated with mycelium which grew out readily when particles of the flesh were placed on agar. The resulting cultures developed sexual organs similar to those found in the other cultures.

Inoculation Experiment 7. Apples and pears were inoculated simultaneously with two strains of the fungus, one isolated from an apple, the other from a pear. The two strains gave identical results; no sporangia were observed in this experiment either on the infected apples or pears, but all produced sexual organs similar to those found on the naturally infected fruit and in cultures.

The morphology of the fungus causing this rot of pears and apples, particularly with respect to the sexual organs and the sporangia, conforms to that of *Phytophthora Cactorum* as given by Rosenbaum(10) who has recently made a comparative study of the genus, and as this fungus has been identified as causing a similar rot on pears and apples on the Continent and on apples in America it is to be concluded that the disease occurring in this country is identical with that found abroad.

Control Measures.

Since the fungus continues to develop on the fallen fruit these should be collected and burnt; fruit rotting on the trees should also be removed and destroyed. These precautions would tend to keep the disease in check by eliminating centres of infection, but in general would only be practicable on a small scale, as in gardens and small orchards.

As the outbreaks hitherto reported in this country have been sporadic and localized, and as the disease appears to be serious only during very wet weather at the time the fruit is approaching maturity, experiments with a view to controlling the disease by spraying have not been attempted. From analogy with other diseases caused by members of the Peronosporaceae it is probable that Bordeaux Mixture would be an effective wash as a preventive against infection, and in fact has been recommended for this disease by Marchal(3). The formula 4 : 4 : 50, i.e. 4 lbs. copper sulphate, 4 lbs. quicklime, to 50 galls. of water, gives a Bordeaux Mixture suitable for pear trees and many varieties of apples, and should be given a trial in the event of a threatened epidemic of the *Phytophthora* rot.

SUMMARY.

In wet seasons *Phytophthora Cactorum* (Lebert et Cohn) Schröter sometimes produces a rot of apples and pears in this country, causing the fruit to fall.

The rot in pears is characterized by a dark brown discoloration of the affected tissues accompanied by the appearance, at the surface, of clusters of sporangia, seen with the naked eye as glistening particles.

In apples the discoloration is paler and sporangia are less readily

produced; frequently the skin splits and the mycelium of the fungus is seen on the exposed surface as a whitish bloom.

To keep the disease in check rotting fruit, whether on the ground or still on the tree, should be collected and destroyed.

BIBLIOGRAPHY.

(1) Bubák, F. Die Phytophthorafäule der Birnen in Böhmen. *Zeitschr. f. Pflanzenkr.* Bd. xx, pp. 257–261, 1910.

(2) Dastur, J. F. On *Phytophthora parasitica* nov. spec. a new disease of the Castor Oil Plant. *Mem. Dept. Agr. India,* Bot. Ser. vol. v, No. 4, pp. 177–231, May, 1913.

(3) Marchal, E. Sur une maladie nouvelle du Poirier. *Bull. Soc. Roy. de Belgique,* 45, pp. 343–344, 1908.

(4) Osterwalder, A. Die *Phytophthora*-Fäule beim Kernobst. *Cent. f. Bakt.* Abt. 2, Bd. xv, pp. 435–440, 1906.

(5) —— Von der Obstfäulnis am Baume. *Schweizer Zeitschr. f. Obst- u. Weinb.* pp. 261–265, 1912.

(6) —— *Landw. Jahrb. d. Schweiz,* xxvi, No. 6, pp. 321–322, 1912 (Abs. in *Exp. Sta. Rec.* vol. xxviii, No. 1, p. 54, Jan. 1913).

(7) Pethybridge, G. H. On the Rotting of Potato Tubers by a new species of Phytophthora having a method of Sexual Reproduction hitherto undescribed. *Sci. Proc. Roy. Dublin Soc.* vol. xiii, (N.S.), No. 35, pp. 529–565, March, 1913.

(8) —— and Lafferty, H. A. A Disease of Tomato and other Plants caused by a New Species of Phytophthora. *Sci. Proc. Roy. Dublin Soc.* vol. xv, (N S.), No. 35, pp. 487–505, Feb., 1919.

(9) Robinson, W. "Black Neck" or Wilt Disease of Asters. *Ann. Applied Biol.* vol. ii, Nos. 2 and 3, pp. 125–137, 1915.

(10) Rosenbaum, J. Studies of the genus Phytophthora. *Jour. Agr. Res.* vol. viii, No. 7, pp. 233–276, Feb., 1917.

(11) Schoevers, T. A. C. Het Phytophthora-Rot der Pitvruchten. *Tijdschr. Plantenziekten,* 21 Jaarg. No. 5–6, pp. 153–159, 1915.

(12) Unamuno, L. Los estragos de la Phytophthora Cactorum en las peras y ciruelas. España y America, 1910 (Abs. in *Zeits. f. Pflanzenkr.* Bd. xxi, p. 379, 1911).

(13) Whetzel, H. H. and Rosenbaum, J. The Phytophthora rot of apples. *Phytopath.* vol. vi, No. 1, pp. 89–90, Feb., 1916.

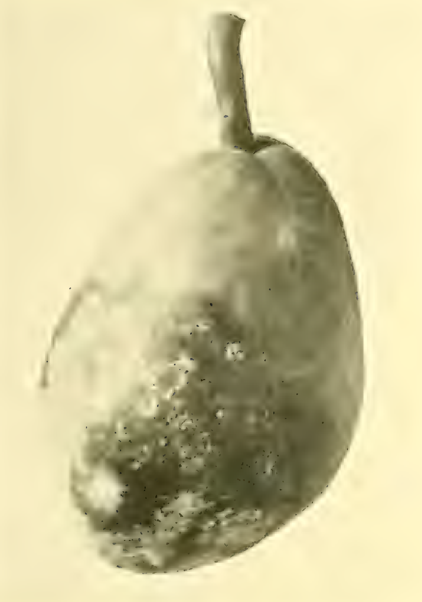
DESCRIPTION OF PLATE III

Fig. 1. A pear 6 days after inoculation with mycelium of *Phytophthora Cactorum* taken from a pure culture.

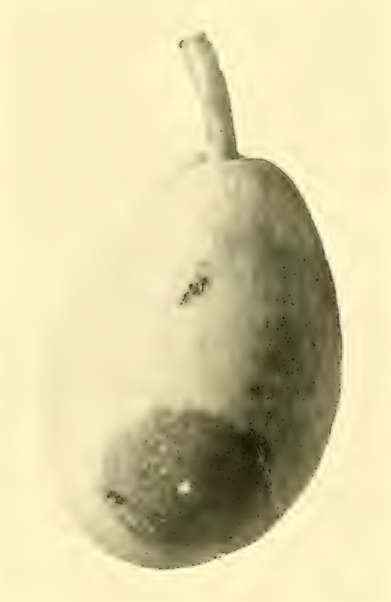
Fig. 2. The same 3 days later; by this time sporangia had developed.

Fig. 3. Apples (var. Lane's Prince Albert) affected with the Phytophthora rot.

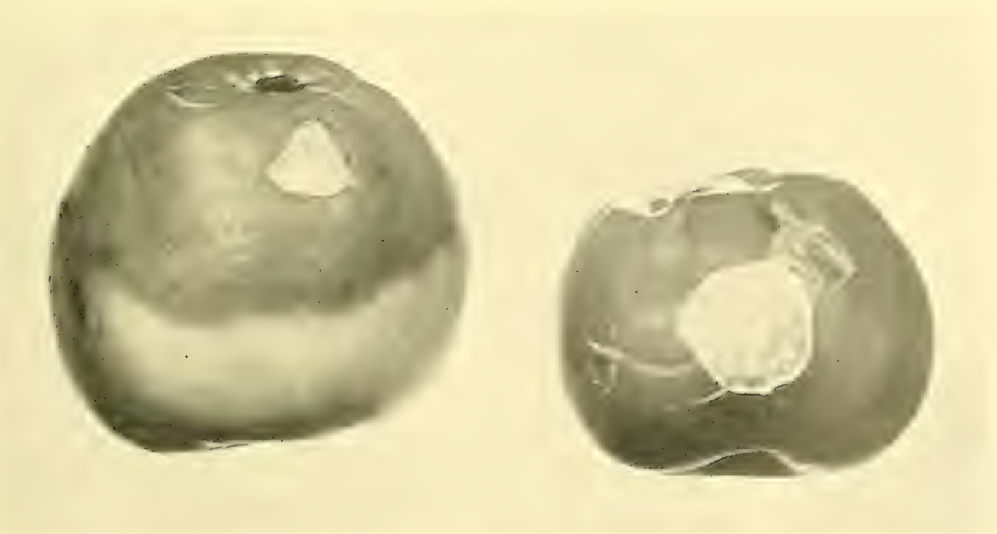
THE ANNALS OF APPLIED BIOLOGY. VOL. VI, NOS. 2 & 3 PLATE III



1



2



3

NOTES ON THE BIOLOGY OF *NECROBIA RUFICOLLIS*, FABR. [COLEOPTERA, CLERIDAE.]

By HUGH SCOTT, M.A., Sc.D. (Cantab.).

(*Curator in Entomology, University of Cambridge.*)

(With 2 Text-figures.)

So much has been written about the subject of this paper that an apology for bringing the matter up again seems necessary. I had, however, opportunity to observe the insect in numbers, and can place on record some observations which are not mere repetition of any hitherto published. During 1917 and 1918, being attached as entomologist to the Hygiene Department, Royal Army Medical College, I worked in the entomological laboratory of the Imperial College of Science, South Kensington, and the observations herein recorded were made in the intervals of routine work. A large room was given up to the breeding of *Musca domestica* for experimental purposes: it was heated by radiators and bunsen burners, and a constant succession of generations of flies was maintained summer and winter alike. This fly-culture had been started late in 1915 (long before my advent at the laboratory) and was kept going continuously till late in 1917. The maggots were fed on a mixture of brown bread, casein and banana, or, late in 1917, of bran, casein and beetroot. The ingredients were thoroughly pounded and mixed, and moistened masses of the mixture were placed in large shallow vessels. The food was surrounded by sawdust in which the full-fed maggots could pupate. As fresh food was added, the lower part of the vessels became full of a mass of débris of old food, sawdust, and countless empty puparia from which flies had emerged. It was in this dark-coloured detritus that the *Necrobia*-larvae lived. They kept below the surface and were not seen unless the débris was turned over. Other denizens of this débris were one or more kinds of *Dermestes* and the moth *Tinea pallescentella*, Stainton. A bug, *Lyctocoris campestris*, Fabr. (= *domesticus*, D. and S.; Anthocoridae), was also present, though only very few of this were found. Occasionally *Fannia*, *Muscina stabulans*, *Drosophila* sp., and a minute Borborid fly[1] also bred in the dishes. Other particulars and photographs of this "fly room" are given by Miss Olive C. Lodge, *Bull. Ent. Res.* IX, p. 142 and pl. VIII–XI (September, 1918).

---

[1] *Limosina minutissima*, Zett. (determined by Mr J. E. Collin).

Necrobia ruficollis was very abundant at the time of my arrival (February, 1917) and onwards. At the beginning of November, 1917, an end was put to the fly-culture, and the room was cleaned and left empty till December 12th, 1917, when a new culture was started. The *Necrobia*, however, survived these weeks of cold and absence of food, and became plentiful again in the new culture. This second culture died out in April, 1918, when for three weeks of very cold weather the room was left without heat and empty of food. The *Necrobia* scarcely survived, for though a third culture of flies was commenced in May, 1918, the beetle was not in evidence again throughout the year, excepting for one small adult seen on June 4th, 1918.

TEMPERATURE. When the heating appliances were in use, the temperature still varied somewhat with season and weather, but was generally between 70° and 80° F. (about 21° and 27° C.). The extremes which I recorded were 64° and 89° F. (about 18° and 32° C.). On some very cold nights the temperature may have fallen even lower. But the *Necrobia* was always active and at these temperatures seemed to continue breeding without intermission, regardless of the season.

Heeger (8) states that in autumn, at 9°–10° (between 48° and 50° F.) the larvae seek sheltered places for wintering, and the adults cease pairing; while at 7°–8° (between 44° and 46° F.) the adults also seek their places for hibernation[1]: and that larvae and adults awake from their winter's sleep at 8°–10°, but only commence pairing, which usually takes place in the middle of the day, when this part of the day has become decidedly warmer.

FOOD OF THE LARVAE. Are the larvae predaceous on maggots, etc., which live in company with them, or do they eat only dead organic matter, or resort to both kinds of diet? As far as my experience went, they could only with great difficulty be induced to kill and eat fly-maggots. This is further discussed below, after a brief review of the conclusions of earlier writers, and of the behaviour of allied species.

Heeger apparently considered them entirely saprophagous, stating ((8) p. 976) that they "suchen weiche Fetttheile, von welchen sie sich auch bis zur Verpuppung nähren." Gallois and Perris, on the other hand, thought that they are predaceous. Gallois, who observed them in great numbers in a bone store in company with *Lucilia*-larvae, remarked that when the *Necrobia*-larvae were abundant the *Lucilia*-larvae were scarce, and vice versa, and Perris ((19) p. 50) quotes him as writing in a letter "cet insecte me paraît être exclusivement carnassier...à l'état de larve, et saprophage...à l'état parfait," while Perris himself came to the same conclusion ((19) p. 51).

---

[1] Kemner (13) considers that the allied *Necrobia violacea* hibernates as an imago. In another allied species, *Necrobia rufipes*, Howard ((11) p. 106) quotes Riley ((21) p. 95) to the effect that at St Louis there are several generations annually but that the winter is invariably passed in the larval state.

Taschenberg ((25) p. 16) thinks that the larvae of *N. ruficollis* have gradually given up the predaceous habit (the general habit of the Cleridae) and adopted saprophagous habits, but that sometimes they return to their primitive ways, killing and devouring fly-larvae. Cholodkovsky (1) appears to be much of the same opinion. This probably is a correct view of the case, and the observations recorded below tally with it.

The most usual habitat of *Necrobia* seems to be among bones, carrion, dried meat, skins, etc. Many writers have stated this, Curtis especially (3) emphasising that *Necrobia* differs in this respect from all the rest of the Cleridae, including *Corynetes*: all of them undergoing their metamorphoses in wood. *Necrobia* has been found more than once among insects discovered in Egyptian mummies (5, 27). It has occurred as a human parasite, a curious and probably quite abnormal case being recorded by Houlbert (9); a small larva, alive and active, was removed from a cyst in the eye of a girl of 14 years, in France. Maxwell-Lefroy (17) states that *N. ruficollis* is known to be destructive to the dry cured fish prepared in Sylhet. Kemner ((13) p. 201) found the larvae of *N. violacea* on carrion, and thinks they are probably predaceous on other larvae. Le Conte (15) in 1848 recorded this same species as covering the ground under any small piece of animal matter in the "barren regions adjoining the Rocky Mountains." Houlbert and Bétis (10) record observations to the effect that *N. violacea* and *N. ruficollis* complete the destruction of carcases commenced by Silphids and *Dermestes*. Howard (11), describing the habits of *Necrobia rufipes*, the "red-legged ham beetle," mentions no kind of larval diet except dried animal matter. I recently found a number of larvae of *N. rufipes*, in various stages of growth, on the top surface of the contents of cases of dried egg, imported from the Far East: several other species of beetles and their larvae were present[1].

---

[1] Since the above was written, I have seen several references to *N. rufipes* in *Rev. Appl. Ent.*, Ser. A, VI, 1918. On pp. 128 and 539 are records of its being found (in Zanzibar and Ceylon respectively) in the larval and adult states in stored copra, to which it is said to do serious damage. On the other hand, on p. 68 is an allusion to it as breeding (in the Seychelles) everywhere in salt fish, and in this case its presence in copra was regarded as accidental, due to storage of the copra and fish in the same room.

The mode of life of *Corynetes coeruleus* is distinct from that of *Necrobia*. As already mentioned, it has the normal wood-frequenting habits of the Cleridae, and the fact that it preys on Anobiids has been recorded by a number of writers (see Curtis (3) and remarks thereon by Westwood (27): also Perris (19, 20), Sharp (22), Houlbert and Bétis (10), Kemner (13), Moll (18)). These all refer to *C. coeruleus*, de Geer, or *C. ruficornis*, Sturm, which is a synonym thereof according to Schenkling (Col. Cat., Cleridae, 1910).

I tried to get actual proof that the larvae of *Necrobia ruficollis* kill fly-maggots, by isolating them, singly or in twos and threes, in small lightly-covered vessels containing a little sawdust in which the larvae could hide, and placing with them eggs or maggots of various ages of *Musca domestica*, or puparia (either sound or pierced with a needle so that the juices exuded) of *Musca* or of blowflies. The vessels were kept in the dark, as the *Necrobia*-larvae shun light. But, though no other food was provided, in none of my many experiments would the *Necrobia*-larvae attack and eat living eggs, maggots, or puparia of flies: they seemed to prefer to starve, and in some cases actually died, though whether primarily from starvation or desiccation is uncertain. But at a later date it fell to Mr R. E. Tooke, who was then working at the Imperial College, to watch some larvae, which he had isolated, in the act of killing and devouring fly-maggots: this is referred to more fully below.

As a result of these isolation experiments it appeared that: (i) the larvae probably eat the exuviae, etc., out of empty puparia from which flies have emerged; (ii) they sometimes ate their way into unbroken puparia containing fly-nymphs; (iii) they ate the soft parts of dead adult flies; (iv) they were attracted to mouldy cheese; (v) in some cases they killed, and ate the soft parts out of, fly-maggots; (vi) there was no actual proof of cannibalism, though it may have occurred in some cases where several larvae were together.

Headings (ii), (iii) and (v) are worth discussing more fully.

(ii) *Boring into intact puparia.* Perris ((19) p. 51) records finding a few puparia quite intact except for a little round hole through which the *Necrobia*-larva had entered prior to pupation within the puparium. Gallois (7) found in a sand-heap puparia of *Lucilia* which had been broken into at the head end by larvae of *Necrobia ruficollis* desirous of pupating; this caused the *Lucilia*, if fully developed, to try and break its way backwards out of its puparium at the hind end (in which effort it generally died), or, if in a less advanced stage, the *Lucilia*-nymph was crushed against its puparium and killed by the invading *Necrobia*-larva. Gallois, however, says nothing about the *Necrobia*-larva actually *eating* the nymph of the fly. Taschenberg (25) apparently made no observation of the *Necrobia* eating into intact puparia.

On 11. iv. 1917 I placed four partly grown *Necrobia*-larvae in a vessel with a number of sound puparia of *Musca domestica* and no other food; I failed to examine them again till 2. v. 1917, by which time two of the *Necrobia* had pupated and the other two had disappeared, but five puparia had been broken into, one in two places, and cleaned out.

In the two following cases the *Necrobia*-larva was watched in the act of boring its way into an intact puparium of *Musca domestica*. My attention was drawn to one of them by Mr Ll. Lloyd, who discovered the larva in the act. In one of these cases the contained nymph may have been dead, though the puparium was intact. The first of these two *Necrobia*-larvae looked about two-thirds grown, and was found—not in one of the small vessels, but in a big vessel containing a mass of fly-maggots, food, and débris—entering the puparium (which was a small one) through a small hole on the left side of the 2nd and 3rd segments, dorso-lateral in position. Being disturbed, the larva backed out of the hole, but soon started in again, and got its whole body inside, the terminal segment and brown chitinous hooks disappearing after a few moments. During the next two hours it could be seen through the hole, moving about inside. For the next 3 days it remained in the puparium, the hole being blocked by a projecting mass of pellets of moist brown frass. When next looked at, 6 days later, the larva had come out again, having about doubled the size of the hole by eating away the substance of the puparium irregularly towards the anterior end. The puparium was absolutely cleaned out, no trace of nymphal substance being left in it. The *Necrobia*-larva was found dead a fortnight later, having refused several other kinds of food. The second larva was found (21. ii. 1917) entering a larger puparium by a hole much further back, in the 4th and 5th segments. At intervals up to 2. iii it could be seen moving about inside, the hole not being blocked; on 15. iii the hole was found blocked, and by 17. iii it was covered with the screen of hardened white secretion made by the *Necrobia* before pupation.

(iii) *Eating dead adult flies.* Several houseflies emerged from puparia in the small vessels with the *Necrobia*-larvae, and died in the vessels. Their remains were found with the soft parts of thorax and abdomen eaten out, and heads, wings and legs scattered about. [Adult *Necrobia* also ate dead flies; see below.]

(v) *Killing and eating fly-maggots.* As stated above, in none of my experiments in 1917 could the *Necrobia*-larvae be induced to attack living maggots of any age. But early in 1918 Mr R. E. Tooke watched them in the act. His observations may be recorded in his own words:

"Several larvae were placed in a receptacle containing sawdust and were left for about 24 hours without food. Two fly-larvae were then placed in the receptacle. For some time, although the *Necrobia*-larvae frequently came into contact with the fly-larvae they did nothing more than open their mandibles, more as a defensive than an offensive action. It was not until one of the fly-larvae crawled over a *Necrobia*-larva, that there was any definite attempt on the part of the latter to seize the fly-larva. Even then it seemed to be an act of defence rather than of aggression. In the resulting struggle the *Necrobia*-larva hung on tenaciously; eventually the skin of the fly-larva was ruptured and it became quiescent, and the *Necrobia*-larva commenced eating it. The soft parts were eaten out leaving the empty skin. The other larvae of the beetle also took part in eating the dead maggot, even though the second maggot was still actively moving about the vessel. This maggot was ultimately killed and eaten in the same way as was the first. Live maggots placed with other *Necrobia*-larvae were also killed and eaten. *Necrobia*-larvae were often seen to attempt to seize mites, but seemingly without success."

PUPATION. Heeger(8) speaks of the "unverhüllte Verwandlung zur Puppe." In one experiment, certainly, two of my larvae did pupate fully exposed, lying on their backs, on the sawdust in a small vessel: but these had probably been subjected to unfavourable conditions, having refused several kinds of food offered to them. Normally the larvae either make a cell and line it with a hardened, opaque, white secretion, or make use of some existing cavity—notably the interior of a fly-puparium—screening all openings over with the white secretion.

The very frequent use of empty puparia of flies has been discussed by several writers (Perris, Gallois, Taschenberg, Kemner [p. 200]). I found this to be quite the favourite place for pupation, puparia of *Calliphora*, *Phormia coerulea*, and *Musca domestica* all being used. In the case observed by Gallois the puparia were those of *Lucilia*, while in that recorded by Taschenberg the fly is said to have been *Calliphora azurea*, Fallen[1]. The end of the puparium where the fly has emerged is screened over with a wall of the white secretion, or in the few cases where a larva has been seen to bore into an intact puparium, its entrance-hole was covered in the same way (Perris, and *ante*, p. 105). The inner surface of the puparium itself is not lined.

---

[1] *Protocalliphora* (or *Avihospita*) *azurea* (Fallen) is a rather scarce fly, the larvae of which have been found infesting nestling birds. Probably what is really meant is *Phormia coerulea*, R.-D., frequently but less correctly referred to as *Protocalliphora groenlandica*, Zett., a species which often breeds in profusion in bone factories and other places where dead animal matter accumulates.

In my experiments there seemed to be some preference of the larvae for the more roomy blowfly-puparia, and beetles emerging from these were on the whole larger than those which had pupated in puparia of *Musca domestica.* No puparium was ever found to contain more than one *Necrobia.*

Other places besides empty puparia are used. Kemner (p. 200) cites the observations made in the Danish Zoological Museum, where larvae of *N. ruficollis* pupated not only in empty puparia of flies, but in cast larval skins of *Dermestes*, closing them with the white secretion. Kemner also quotes Lampert (14) as recording the finding of larvae of *N. ruficollis* in cork, the larval passages being closed with secretion: Kemner thinks these larvae were probably preparing to pupate in the cork, just as did those of *Corynetes* and *Opilo* kept in captivity by him.

One of my larvae pupated in a crevice in a piece of dried banana, closing the opening with the white secretion. When nothing else was available, or even in some cases where empty puparia of *Musca* were available, the *Necrobia*-larvae readily constructed cells in sawdust. They plunged down into the sawdust provided for them in small vessels, made winding burrows, and after a few days had excavated hollows, nearly always in the angle formed by the bottom and sides of the vessel. These hollows they lined with the white secretion, which held the surrounding grains of sawdust together, thus forming a cocoon which could be removed intact. Only the part of the wall of the cell formed by the glass was left uncoated with sawdust or secretion, with the result that the larvae and pupae could be seen within their pupal cells. In these cells the larvae lie not fully extended, but slightly curved. The excavation and lining of the cell appeared to take some time. Occasionally larvae were seen in cells which they had not begun to line, and once a larva was observed in a partly lined cell, with gaps in the white coating, which were not filled in till the following day.

Certain allied species make cocoons of the same type. Howard (11) describes *Necrobia rufipes* as forming papery cocoons, after boring into the muscle of hams on the fat of which the larvae had been feeding, or into neighbouring woodwork[1]. Mangan (16) also describes and figures cocoons formed by this species in bales of cotton. Information about *N. rufipes*, with small figures of its larva, pupa, and cocoon, is also given by Riley(21) and Smith(23). Kemner records that a larva of *Necrobia violacea* made itself a hollow in the cotton-wool stopper of the tube in which it was imprisoned, used its secretion also, and pupated in the cell thus formed. Perris writes of *Corynetes coeruleus* (= *ruficornis*) lining its pupal cells with white secretion: and Kemner describes how a larva of the same species, in captivity, excavated itself a hollow in the cork of the vessel, and lined the hollow with shining white material.

---

[1] Compare Kemner's account of the boring of wood and cork by *Opilo domesticus* and *Corynetes.* A larva of *Dermestes* which I placed in a small bottle in 1917, bored about half an inch into the cork, and pupated in the burrow.

Though I once watched a larva, through the side of a glass vessel, turning about in its partly lined cell, and working over the walls with its mouth, I could not see whether the secretion was being actually produced from the mouth, and have found no decisive statement in the literature as to how it is produced[1].

Heeger gives 12–14 days as the duration of the pupal stage. My somewhat incomplete data indicate about 20 days as the period from the making of the cocoon to the emergence of the adult. This was at rather lower temperatures than those mentioned on p. 102, since I kept the vessels in which the larvae pupated in a room less strongly heated than the fly-room. But the larva may not become a pupa immediately after the completion of its cell, and the adult after its transformation remains in its cell for some time (a matter of days in some cases) before emerging; this could be seen, in the sawdust-cocoons, through the glass sides of the vessels. On one occasion when a number of puparia of *Musca* occupied by *Necrobia* were broken open, immediately the adult beetles, with fully developed colouring, ran actively out. Kemner ((13) p. 199) found that the pupal stage of *Corynetes coeruleus* (in captivity) lasted about a month.

HABITS OF ADULT BEETLES. Besides running actively, in the warm breeding-rooms the beetles frequently flew. They did not shun light as completely as do the larvae, for, though frequently found under masses

[1] Taschenberg (*l.c.*) makes some remarks on the composition of the white secretion and cites Girard (*Traité élémentaire d'Ent.* vol I, 1873, p. 541) to the effect that Clerid larvae pupate in cells which they line with a secretion which appears to exude ("suinter") from the body, and that they collect it by scraping the abdomen with the mandibles. How far this is correct I cannot say; it does not sound very probable. Cholodkovsky (1, 2) describes and figures two large roundish glands, opening one on either side of the anus in the adult *N. ruficollis*: can they be larval secreting glands persisting in the adult? Perris ((19) p. 51) supposed the secretion to be from the anus. Kemner ((13) p. 197) thinks that in *Opilo domesticus* it comes from the mouth, because he always found the head turned towards the lid of the pupal cell, which lid is formed by the larva out of fragments of wood cemented together by the secretion.

of fly-food, etc., they also flew, ran and fed in bright light and exposed places. They appeared to eat a variety of things including dead maggots, puparia, and dead flies; possibly also the fly-food, and mouldy cheese (which they frequented in large numbers); while they repeatedly visited a shallow dish of very weak sugar-solution. The evidence was against their *killing* fly-maggots, as the following records of observations show:

29. v. 1917. A beetle was twice seen to seize a living half-grown *Musca*-maggot, both times dropping it and finally leaving it alive; the beetle then seized a second maggot, held it a few moments, then dropped it and left it also alive.

19. iv. 1917. A number of adult *Necrobia* were seen eating dead, small, partly grown, blowfly-larvae. In one place four beetles were busy on a single maggot, and during part of the time that they were watched as many as six were there; in a second case another three or four beetles were also busy on a single dead maggot. The working of the beetles' jaws was watched, and they did not appear to tear the maggots, but somehow to extract all the soft parts and leave the flabby, empty, skins to all appearance intact. The eagerness with which the beetles crowded to these two dead maggots, though there were in the same vessel large numbers of living ones of all sizes, leads one to suppose that they do not readily kill maggots; from what cause the two dead maggots had died is not known.

4. v. 1917. Three or four beetles seen greedily eating the soft parts of a blowfly-pupa, the puparium of which was broken open in some way (not, I think, by the beetles).

On another occasion three *Necrobia* emerged from the pupal stage in a small vessel. A sound puparium of *Phormia coerulea* had been opened along the same sutures as those used by an emerging fly, and the dried, mummified remains of the fly-nymph were found lying at a little distance from the empty puparium. This case is enigmatic: the puparium had not been opened before the beetles pupated, and the fly-nymph did not look developed enough to have emerged of its own accord. Could the beetles have broken open the puparium along the normal lines of weakness, and dragged out the nymph?

1. v. 1917. An adult *Necrobia* watched eating the soft parts of the abdomen of a dead blowfly, which was lying on its back; two others near it had also had their abdomens eaten out.

29. v. 1917. Two of the beetles seen eating one dead, newly-emerged housefly: no proof as to whether they had killed it or not.

NOTES ON THE LARVA AND PUPA.

The Egg is described and figured by Heeger ((8) pl. VIII, fig. 13).

Larva (fig. 1): this is fully described and figured by Heeger; Perris also describes it ((19) p. 51), and gives outlines of the terminal hooks in lateral view and of the ocelli ((19) pl. VII, figs. 243–4). Heeger's figure shows the larva as broadening markedly behind the middle, this is more noticeable in some specimens than in others, depending partly on the degree of extension of the segments. Fig. 1 shows a larva which had died with the first three abdominal segments retracted and the others much extended. The dark and light mottlings are somewhat asymmetrical and variable, but in my material there is always a fairly well-marked mid-dorsal pale line, broadening in the middle of each segment, and continuous from the eighth (penultimate) forwards to about the third abdominal segment: in front of this it becomes broken up and irregular. Heeger's figure does not show this arrangement of markings. The ventral surface is much paler, with the dark mottlings very faint, but still discernible. Ventro-lateral regions very pale, but a marked dark patch on either side nearer the front margin of each segment.

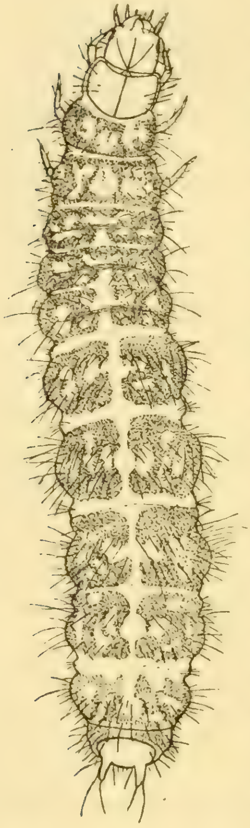


Fig. 1. × approx. 10.

The *setae* in my material are yellowish or reddish testaceous. They are more numerous than those shown in Heeger's figure, there being two bands of setae across the dorsum of each abdominal segment (at any rate in segments 1–7), and the setae of each band not always standing in a single row. In Fig. 1 they are indicated, but it is not attempted to show every one. They are more numerous in the dorso-lateral regions, where they include some very long ones. There is a small group laterally in the constriction between each two segments. Ventrally the segments appear at first sight bare, but with a high power two bands of very short setae can be seen extending across, and a group of slightly longer ones on either side.

The *terminal chitinous hooks* closely resemble those of *Necrobia* *violacea* as figured by Kemner ((13) p. 206). He figures these structures in five genera of Cleridae. There is a marked difference between the pointed hooks of *Necrobia*, and their blunt truncated form in *Corynetes coeruleus*. Perris ((19) p. 52) remarks a similar difference in comparing the hooks in *N. ruficollis* with those of *Corynetes ruficornis*.

CHANGES IN SETAE AND COLOURING DURING GROWTH OF LARVA. This point does not seem to have been investigated before, but two young larvae in my material indicate that such detailed changes do occur, as might be expected. These young larvae are 4·25–4·5 mm. long (the full-grown one figured is circa 10 mm.).

The first has the head, prothorax, and tail-plate well chitinised, and of much the same colour as in the full-grown larva. The dark markings on the dorsal surface are rather sharply contrasted with the pale areas, and the arrangement of light and dark is different from that in the full-grown larva; there is no continuous pale mid-dorsal line even on the posterior segments, the dark area being continuous across the posterior part of all the segments, and across the anterior part of the meso- and meta-thorax and first two abdominal segments; the general disposition of the pale markings is to form a *transverse* rather than a longitudinal light mark across the middle of each segment. The setae are of great length in proportion to the breadth of the body, some being as long as that breadth, and these long ones occurring dorsally as well as dorso-laterally. There are short setae as well and the general arrangement appears to be in two transverse series on each segment, as in the full-grown larva.

The second small larva shows more marked differences from the full-grown larva. Its setae are differently disposed to those of the young larva just described, and it probably belongs to an earlier instar. Its head, prothoracic and tail-plates appear less strongly chitinised and are paler. The whole larva is paler, the dark markings being very faint, and not nearly as sharply contrasted with the pale, and having the appearance of faintly dusky areas of fine dots. The setae are much less numerous; very long ones occur both dorsally and dorso-laterally, but the short ones are comparatively few. The two transverse series can be discerned on each segment, but each consists of but a single row very widely spaced; each row appears to be composed, dorsally, of three very long ones, a median and two lateral, with very few, or sometimes no, shorter ones between them.

The PUPA is figured and described by Heeger. Fig. 2 is made with a drawing apparatus from one of 14 pupae which I preserved. This example is about 5·25 mm. long: the apparent asymmetry of its head in the figure is due to its having lain in a slightly oblique position. The most striking thing about all the pupae of my material is the dark pigmentation of the abdomen, contrasted with the paleness of the other parts. Heeger does not mention this. It is indicated in my figure, but is much more noticeable on the dorsal side, where it extends all the length of the abdomen (being more concentrated laterally and towards the hind end), and some flecks of dark pigment occur also on the meso- and meta-thorax. This dark colouring is just as marked in those pupae which are less advanced, and still have the eyes quite unpigmented. It was noticed in the live pupae, and is not due to a post-mortem change. It is diffused under the cuticle, and is not due to dark intestinal contents showing through partly translucent tissues.

The long, fine, setae are nearly all dorsal or dorso-lateral in position. The figure indicates the disposition of such as can be seen in ventral view. They do not extend on to the ventral surface, except on the hind margins of the two abdominal segments before the last, and in the anterior of these two they only occur towards the sides. Dorsally they are numerous on the prothorax, few on meso- and meta-thorax: on each abdominal segment there is a pair on the hind margin near the middle line, and there are several in the lateral regions.

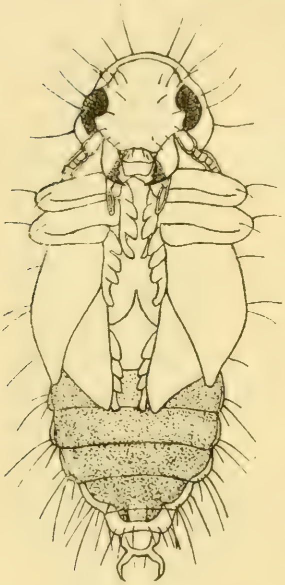


Fig. 2. × approx. 12½.

SUMMARY.

(1) *Necrobia ruficollis* bred abundantly in the "Fly Room" at the Imperial College of Science, London, in 1917–8. The larvae lived in the débris in the vessels in which houseflies were bred. This débris consisted of remains of food provided for the fly-maggots (a mixture of bread or bran, casein, and banana or beetroot), sawdust, and numbers of empty puparia.

(2) During long periods in which the room-temperature was at or above 64° F. (about 18° C.) the *Necrobia* continued breeding regardless of season.

(3) Observations made tend to confirm the view already expressed by some writers, that the larvae of this insect are usually saprophagous, but that they sometimes return to the predaceous habits characteristic of the Cleridae, and kill and devour other larvae. They were observed to eat the soft parts of dead adult flies, and to be attracted to mouldy cheese; they sometimes bore into puparia of flies (two were watched in the act); and with considerable difficulty some were induced to kill and eat fly-maggots.

(4) For pupation the larvae make use of existing cavities, and screen over all spaces with hardened, white, opaque, secretion; or they make themselves cells, and line these with the secretion. As recorded by earlier writers, a very frequent method is to enter an empty fly-puparium, and screen over the open end. But they also readily excavated and lined cells in sawdust, sometimes even when empty puparia were ready to their use. Two larvae pupated without any cell or cocoon, but this was probably a result of unfavourable conditions.

(5) The adult beetles were observed to eat dead fly-maggots and the soft parts of dead adult flies. They were attracted in numbers to mouldy cheese and to sugar-and-water. The evidence was against their killing fly-maggots.

(6) Some notes on the form of the larva and pupa are given, including observations which indicate that slight changes in the number of setae, etc., occur at the larval moults.

REFERENCES.

The following is not intended to be an exhaustive list of every work in which allusion is made to the habits of *Necrobia*. Many of the older text-books and other writings refer briefly to the subject without making any fresh contribution to it, and the titles of these works are not all included. Rupertsberger gives a number of references to articles bearing on the biology of this genus and of *Corynetes* (*Biol. d. Käfer Eur.* 1880, p. 172; *Biol. Lit. d. Käfer Eur.* 1894, p. 176): so also does Schenkling (*Coleopterorum Catalogus*, Part 23, Cleridae, 1910, pp. 140, 142, 143). Most or all of these are included in the list below.

References to the history of the association of *N. ruficollis* with Latreille's escape from prison during the French Revolution may be briefly summarised as follows: Latreille alludes briefly to it, *Gen. Crust. Ins.* I, 1806, p. 275, and at greater length, *Hist. nat. Crust. Ins.* IX, p. 157. A fuller account, mainly from Bory de Saint Vincent, is given by Brullé, *Hist. Nat. des Ins.* vol. VI (= Coleopt., vol. III): this is cited *in extenso* by Girard, *Traité élém. d'Ent.* I, 1873, p. 546, and in Künckel d'Herculais, French edition of A. E. Brehm, *Merveilles de la Nature*, vol. VII, Ins. pp. 242–4 (Paris, 1882); it has also been quoted more or less fully by various other writers.

I am greatly indebted to Mrs H. Woods, of Cambridge, for writing me out a translation of Kemner's work, which is in Swedish.

(1) CHOLODKOVSKY, N. *Necrobia ruficollis* à St-Pétersbourg. *Rev. Russe d'Ent.* XIII, 1913, pp. 103–106.

(2) —— *Necrobia ruficollis* in St Petersburg. *Zool. Anz.* 42, 1913, pp. 529–531.

(3) CURTIS, J. *Brit. Ent.* VIII, 1831, Pl. 350 and 351.

(4) DALLAS, W. S. *Elements of Entomology: an outline of the natural history of British Insects*, 1857, p. 119. [Brief references and account of the association of *N. ruficollis* with Latreille.]

(5) ESCHER-KÜNDIG, J. Funde von Insekten in der Schädelhöhle einer Mumie. *Mitt. Schweiz. Ent. Ges.* XI, 1907, pp. 238–242.

(6) FROGGATT, W. W. *Australian Insects*, 1907, p. 169.

(7) GALLOIS, J. Note sur les moeurs du *Corynetes ruficollis*, Ol. et de sa larve. *Bull. Soc. Etud. Sci. Angers*, 4 and 5, 1874–5, pp. 74–80.

(8) HEEGER, E. Beiträge zur Naturgeschichte der Kerfe. *Oken's Isis*, 1848, pp. 974–979, Pl. VIII, figs. 13–22.

(9) HOULBERT, C. Sur une larve de Coléoptère [*Necrobia* Latr.] parasite de l'oeil humain. *Arch. Parasit.* XIII, 1909, pp. 551–554, 3 text-figs.

(10) HOULBERT, C. and BÉTIS, L. Faune Entomologique Armoricaine: Cleridae. *Trav. Sci. Univ. Rennes*, IV, 1905, 1er Suppl. pp. 134–135.

(11) HOWARD, L. O. The Red-legged Ham Beetle (*Necrobia rufipes*). In "The principal household insects of the United States," *U.S. Dep. Agr., Bull.* IV, 1902, pp. 105–107, figures.

(12) *Insect Life*, IV, 1892, p. 203.
[Note on finding of larvae of *Necrobia* in plush: it is considered that if this was not merely accidental, they might have been feeding on clothes'-moth larvae.]

(13) KEMNER, A. Våra Clerider, deras lefnadssätt och larver. *Entomologisk Tidskrift*, 34, 1913, pp. 191–210. [Abstract in *Rev. Appl. Ent.* Ser. A, II, 1914, p. 100.]

(14) * LAMPERT, K. Bilder aus dem Käferleben. *Naturwiss. Wegweiser*, Ser. A, 2, p. 51.

(15) LE CONTE, J. L. On certain Coleoptera, indigenous to the Eastern and Western Continents. *Ann. Lyc. Nat. Hist. New York*, IV, 1848, p. 162.

(16) MANGAN, J. The occurrence of *Necrobia* and *Dermestes* in Cotton Bales. *Jour. Econ. Biol.* (London), VI, 1911, pp. 133–138, 4 text-figs.

(17) MAXWELL-LEFROY, H. *Indian Insect Life*, 1909, p. 326.

(18) * MOLL, F. Ueber die Zerstörung von verarbeitetem Holz durch Käfer und den Schutz dagegen. *Naturwiss. Zeitschr. f. Forst- u. Landwirtschaft*, Stuttgart, XIV, Nos. 10–11, Oct.–Nov. 1916, pp. 482–503. [Abstract in *Rev. Appl. Ent.* Ser. A, V, 1917, pp. 280–281.]

(19) PERRIS, E. Larves des Coléoptères. *Ann. Soc. Linn. Lyon*, XXIII, 1876 (publ. 1877), pp. 44–53, figs. 242–4.

(20) PERRIS, E. Nouvelles promenades entomologiques (note on *Corynetes ruficornis*). *Ann. Soc. ent. France*, (5), VI, 1876, pp. 188–189.

(21) * RILEY, C. V. *6th Rep. Noxious Ins. Missouri*, 1874, p. 96 [concerning *N. rufipes*, with figures].

(22) SHARP, D. *Cambridge Natural History*, VI, 2nd ed. 1901, pp. 253–254.

(23) SMITH, J. B. *Insects of New Jersey*, 1900, p. 266 (suppl. to *27th Ann. Rep.* (for 1899) *of New Jersey State Board of Agr.*) [small figures of larva, pupa, cocoon, and adult of *Necrobia rufipes*].

(24) STEPHENS, J. F. *Ill. Brit. Ent., Mandib.* III, pp. 326–328, 1830.

(25) TASCHENBERG, O. Beitrag zur Lebensweise von *Necrobia* (*Corynetes*) *ruficollis*, F., u. ihrer Larve. *Zeitschr. wiss. Insektenbiol.* II, 1906, pp. 13–17.

(26) WEST, W. *Necrobia violacea* in a brick wall. *Entomologist*, II, 1865, p. 345 [note on large numbers of this insect in the crevices of a wall near a flue].

(27) WESTWOOD, J. O. *An Introduction to the modern classification of insects*, vol. I, 1839, pp. 266–268, fig. 29, 17.

(28) XAMBEU. Moeurs et Métamorphoses des insectes du groupe des Clerides. *Le Naturaliste*, 30, 1908, p. 152.

* Works of which I have been unable to consult the originals, but have seen abstracts in other writings, are marked with an asterisk.

ON THE LIFE HISTORY OF "WIREWORMS" OF THE GENUS *AGRIOTES*, ESCH., WITH SOME NOTES ON THAT OF *ATHOUS HAEMORRHOIDALIS*, F.

PART I.

By A. W. RYMER ROBERTS, M.A.
(*Rothamsted Experimental Station.*)

(With 5 Text-figures and Plate IV.)

INTRODUCTION.

At the beginning of 1916 the necessity for increased crop production caused by war conditions, with which we had then been faced for some eighteen months, brought forward the constantly recurring "wireworm" problem more acutely than ever. Farmers were being urged to plough up more grass-land for the production of cereals and potatoes; but the reply constantly met with was that if the grass-land were ploughed up, the farmer had no security of harvesting a crop, owing to the probability that the wireworms, which were supposed to exist in great numbers in all old grass-land, would at once concentrate their attention on the crop as soon as it began to grow. The force of this reply was manifest to those who had had experience with the pests. Our knowledge of the life history, or even of its duration, was incomplete, while it was felt that none of the methods of control usually recommended could be relied upon to form a complete rejoinder to the objection of the farmer to altering his system of cultivation.

In these circumstances it was decided by the authorities at Rothamsted to make an attempt to supply some of the missing facts and work was accordingly begun in the same year.

The present paper represents the results obtained in the biology and life history of *Agriotes*, while it is hoped in the future to publish those obtained in the internal anatomy of the larva and on the research made to secure an adequate insecticide for control purposes.

Many details are still incompletely known, but as certain points of the life history have in some measure been cleared up, it has been felt that these should be put on record without further delay.

To Dr E. J. Russell, the director of the Station, for the opportunity to carry on the work, also to Mr J. C. F. Fryer and Dr A. D. Imms, in addition to Dr Russell, for suggestions and information at many different points, my hearty thanks must be here expressed.

METHODS.

In order to obtain eggs from the parent beetles, grass plants were potted up in small (4 inch) pots and the surface of the pots enclosed by glass cylinders, the tops of which were covered by a piece of butter muslin. The beetles, when available, could be placed in the cage so formed either by removing the muslin covering the top of the glass cylinder, or by removing the whole cylinder, afterwards pressing it down a little into the soil of the pot, when replaced in position. In this manner the beetles were safely enclosed and by keeping the pots in a shady place and watering sufficiently for the needs of the plants, eggs have been obtained from *Agriotes obscurus* and *A. sputator* in 1916 and from the same two species, with the addition of *Agriotes sobrinus* and *Athous haemorrhoidalis*, in 1918. The pots, after having received their full complement of beetles, were left alone for three or four weeks to allow the beetles time to deposit their eggs without disturbance.

When it was judged that sufficient time had elapsed, the soil was carefully turned over with the point of a penknife and the eggs (if found) were laid bare. Discovery is facilitated if the soil is of a dark colour, is friable and does not contain many grains of sand, which may be mistaken for solitary eggs.

When eggs were obtained, they were taken into the laboratory and placed on damp soil in watch glasses or similar vessels for further observation. The soil being kept moist, no difficulty was experienced in hatching out the larvae. In some cases it was found necessary to pack the eggs for travel and this was done by transferring them to corked tubes containing fresh, moist, moss. Even when kept in these tubes with a bung of moss to replace the cork, for a fortnight or so, the results were satisfactory in the numbers hatched, though the ova appeared to run some risk from moulds which were inclined to spread their hyphae over the moss.

Beside the eggs which were taken from the pots for examination and observation in the laboratory, others remained and hatched in the soil of the pots. During the autumn of 1916 in view of the approaching winter conditions and in order to give the larvae more scope for movement, the soil and grass plants from the small pots which contained larvae were bodily transferred to larger glazed earthenware pots containing more soil. These pots are the usual long pots used at Rothamsted for botanical and other pot work. They measure some 15 inches in length, 5 inches in diameter, and have a lateral bung-hole about one inch from the bottom. It was intended to sink these pots in the soil, bringing the soil-level in the pot to that of the surrounding ground. After experiment, however, great difficulty was experienced in draining the water from the pots without risk of the larvae escaping, so the pots were dug up and transferred to a lean-to shed facing North. Here they remained during the winter and the larvae, at least those of *Agriotes obscurus*, have successfully withstood the rigour of three winters under these conditions. In the summer the pots were transferred to the open and watered sufficiently to keep alive the plants of grass growing on the surface. For the first eighteen months no further supply of food was introduced, but in the spring and summer of 1918, a few slices of potato were given and have been eaten by the larvae.

In addition to the larvae bred from the egg, wild-caught larvae have been kept, in the laboratory chiefly, for observation. Owing to their predilection for a diet of their own kind, especially at times of moulting, it has been found necessary to keep each individual larva separate. Round tin "pill-boxes" or "salve boxes" have been used for this purpose, each larva being placed in a piece of turf or soil and supplied with food from time to time. It is necessary however to exercise care in giving sufficient water, for, as is well known, wire worms are excessively prone to desiccation and the soil must not therefore be allowed to become dry.

It is not pretended that these laboratory-reared larvae are reared under anything approaching natural conditions, but certain points have been elucidated by this method and wherever there is reason to doubt that observations made under such conditions would be different in the field, they can usually be checked.

I have obtained larvae from several different sources, the principal ones, beside the local ones of Harpenden, being Cambridge and Windermere.

From the latter place an almost unlimited supply has been obtained from heaps of stacked sods, originally taken from a meadow on its conversion into garden. Many pupae and newly emerged adults, principally of *Agriotes obscurus*, have also been taken from the same place.

Definition of the word "Wireworm."

Many farmers and gardeners, even yet, use the word "Wireworm" in a loose way to include millipedes and centipedes as well as the larvae of *Elateridae*. The two former must obviously be excluded, and the only question that arises in regard to the name is as to how many of the latter should be included.

In many papers on applied entomology, both in America and in this country, the term has been used to denote the larva of any Elaterid which is known to be destructive to crops. Curtis (7) himself uses it in this way; in one place (p. 153) speaking of eleven species of wireworms, though eventually (p. 189) he refers to the "true wireworms" as *Agriotes lineatus*, *A. obscurus*, *A. sputator* and *Athous haemorrhoidalis*. Westwood (25) in his *Classification* (p. 237) refers to *Agriotes lineatus* and *A. obscurus* as "the wireworm," being in some doubt whether the latter is specifically distinct from the former. He says they (i.e. the wireworms) are so called from "their cylindric form and hard texture." This definition was meant of course to apply to the two species named only, but it is equally applicable to the other species of the genus. It does not apply to an equal extent to species of other Elaterid genera which may be classed as "pests." Following Westwood therefore, the name should belong exclusively to the genus *Agriotes*.

Since, however, the word has been so generally used in recent years to denote the larva of any injurious Elaterid, it seems undesirable to define it any more closely than did Curtis, but to use it as applying primarily to the larva of the genus *Agriotes* and to that of *Athous haemorrhoidalis*, F. The larvae of other species of Elaterids may eventually also have to be included, such as those of *Athous hirtus*, Hbst. (*niger* of Brit. Cat.) and *Corymbites cupreus*, F.

The principal distinguishing characters of *Agriotes* larvae are as follow:

(i) The presence of a tooth, situated dorsally, on the inner edge of the mandible, near its apex, and

(ii) the two eye-like pits situated near the base of the 9th abdominal segment. These pits, originally supposed to be spiracles, are now usually referred to as "muscular impressions," e.g. by Ford (11) and Henriksen (15), but are believed to be sensory organs and are here referred to as "sensory pits."

Athous haemorrhoidalis, F. may be distinguished readily from all the species of *Agriotes* in the larval stage by the absence of the characters just mentioned, by its broader and somewhat flattened appearance and by the presence on the dorsal surface of the ninth abdominal segment of a kind of impressed shield, bearing at its posterior end two pairs of prongs or cerci, which give it the appearance of possessing a bifurcated tail.

This shield is present in many other Elaterid larvae; but the orange-yellow colour of *A. haemorrhoidalis* together with the presence on the ninth abdominal segment of a single median sulcus, from which three or four transverse tributary sulci branch on either side, will serve to distinguish it from any larva with which it is likely to be confused, with the exception of *A. vittatus*—a somewhat uncommon species—and *A. longicollis*, which is rather obviously rugose above.

Relative Abundance of Species.

In Cheshire, North Staffordshire and South Lancashire, Ford found that the common "wireworm" is the larva of *Agriotes obscurus*, L. For England certainly and probably also for Wales and Scotland, the same general statement holds good. There appear to be limited districts where *A. lineatus*, L. or *A. sputator*, L. exceed it in numbers, but the predominance of either of these two latter species seems to be quite local.

Athous haemorrhoidalis, F. is a common and generally distributed beetle and to collectors frequently appears to be more common than the common species of *Agriotes*. This is however a mistake, due to the habits of the beetle itself, which flies more readily than the latter and, being found on flowers and the leaves of trees, is more readily taken with a sweeping-net. *Agriotes obscurus*, *A. lineatus* and *A. sputator* are more frequently found upon the ground or in hiding, so that their abundance as compared with *Athous haemorrhoidalis* is somewhat masked.

In order to gain some idea of the relative abundance of the species of *Agriotes* a number of well known coleopterists and economic entomologists were asked for data of adult beetles of the genus in their particular localities.

The following gentlemen have most kindly given me the benefit of their experience: Commander J. J. Walker (Oxford), Prof. G. H. Carpenter (Dublin), Prof. J. W. Carr (Nottingham), Dr W. Evans Hoyle (Cardiff), Dr R. Stewart MacDougall (Edinburgh) and Messrs G. C. Champion (Woking), F. H. Day (Carlisle), J. Davy Dean (Cardiff), J. C. F. Fryer (N. Cambs.), C. T. Gimingham (Bristol), J. N. Halbert (Dublin), B. S. Harwood (Sudbury), J. H. Keys (Plymouth), W. Mansbridge (Liverpool), A. V. Mitchell (Plymouth), W. E. Sharp (Crowthorne, Berks.), H. J. Thouless (Norwich), J. B. Walsh (Jarrow-on-Tyne).

The data obtained serve to confirm that of Fowler (12), from whose book the following extracts within inverted commas are taken, the remaining notes being deduced from information supplied by my correspondents:

Agriotes sputator, L. "Common and generally distributed throughout the south and midland districts of England; not so common further north." The line, north of which the species is comparatively scarce, appears to run through Norfolk, Nottingham and Cheshire.

A. obscurus, L. "Generally distributed and common throughout the kingdom."

A. lineatus, L. "Common and generally distributed throughout the greater part of England, but more local further north." Usually less common than *A. obscurus* or *A. sputator* even in the Midlands and south of England, but locally it is the dominant species, usually in low-lying positions. Such localities are the water-meadows along the Cherwell and Isis at Oxford (Walker), the banks of the river Trent in the Nottingham district (Carr); the salt marshes of the Solway (Day). In the northern Fen District, Mr J. C. F. Fryer tells me it is equally common with *A. obscurus*.

A. sordidus, Ill. "Very local and usually rare."

A. sobrinus, Kies. "Rather local;...not recorded from Scotland." This species also appears to be a southern and midland species. It is "by no means common" in Durham (Walsh) and "scarce" in Cumberland (Day), while it is not recorded in Sharp's *Coleoptera of Lancashire and Cheshire*.

A. pallidulus, Ill. "Generally distributed and common throughout the greater part of the kingdom."

Athous haemorrhoidalis, F. "Very common and generally distributed throughout the kingdom." As already mentioned this refers to the adult; the larva is less common than those of the commonest species of *Agriotes*.

So far as Scotland is concerned, Dr MacDougall reports that *Agriotes obscurus* is the commonest species; he has no record of *A. pallidulus*. In Ireland *A. obscurus* and *A. lineatus* are the only species of *Agriotes* known to occur, but both are widely distributed. Prof. Carpenter and Mr Halbert believe that *A. obscurus* is rather the commoner of the two.

GENERAL LIFE HISTORY AND HABITS.

THE IMAGO.

When newly hatched from the pupa, the adult beetles are of a pale straw colour. From this colour they pass through a stage in which they appear of a reddish-brown colour (similar to the var. *cinnamomeus*, Buys.) and finally, as the chitin becomes hardened, assume the normal coloration of the species. The process of hardening takes some three or four days, during which the beetles remain within the earthen cell.

Most of the soil-dwelling Elaterids appear to remain in the soil during the winter, but as is pointed out in the leaflet of the Board of Agriculture(4), both *Agriotes lineatus* and *A. sputator* have been found during the winter "in tufts of grass, hedge-bottoms or refuse of dykes." In his *Coleoptera of Lancashire and Cheshire*, W. E. Sharp(22) also records *A. lineatus* as "Common in haystack refuse, etc., during winter."

So far as *A. sputator* is concerned, this habit is not universal, the beetles having been turned up in the soil during winter, though they had probably left the pupal cell previously.

In the case of *A. obscurus,* my observations in the open inclined me to the belief that this species also left its pupal cell and hibernated in the neighbouring soil. Good observers, however, have assured me that they have seen the mature beetle in the cell in winter and early spring, so that there may be a difference in habit in this respect between *A. obscurus* and the other two species named. Probably the friable nature of the soil in the locality where my observations were made is responsible for the breaking-up of the cell before the beetle was discovered.

Athous haemorrhoidalis (and it may also be mentioned *Corymbites cupreus*, F.) similarly remains in the soil during the winter, but whether within the cell or not, has not been ascertained.

In the spring the beetles emerge from their winter quarters, according to my observations, about the middle of May. Adrianov(1), observing at Kaluga in Russia, in the same latitude as Yorkshire, came to the conclusion that they had emerged earlier than May. Local climatic conditions may perhaps account for this, but during four years' observation in Hertfordshire, scarcely any *Agriotes* have been found abroad before the 15th May, although in Westmorland *A. obscurus* has been taken under stones in the first half of April.

At the end of May Adrianov found them in great numbers on the rye and wheat plants. Later they appeared on the stems and ears, very active in bright sunlight, and he considers that the pollen of rye is their favourite food. At sunset, or on cold and windy days, he found that they were hiding in the grass, under lumps of soil and so forth.

So far as *A. obscurus* and *A. sputator* (two of the species referred to by Adrianov) are concerned, my observations do not quite coincide with his. Comparatively few specimens of these two species have been taken by sweeping, either on corn or other plants. They have however been taken in great numbers on occasion under heaps of cut grass and it has been noticed that the largest numbers have been taken in dull or showery weather, as might be expected from reading Adrianov's account.

Vassiliev (23) also refers to a similar habit of hiding during the day on the part of *A. lineatus*, but says that the beetles remain in holes made by themselves, especially in hot weather—a habit which has not been observed in this country.

In contrast to the habits of the said three species, *A. sobrinus* and *A. pallidulus* and also *Athous haemorrhoidalis* are commonly taken from leaves and flowers (especially flowers of *Caucalis anthriscus*) by sweeping growing corn, clover and hedgerow plants. As to the food taken by the adults, little has been observed. *A. sobrinus* and *A. pallidulus* are evidently feeding on the nectar when found on *Caucalis* and *A. sputator* has been observed to do the same in the laboratory, though it is so seldom found on flowers in the field. Vassiliev supposed that *A. lineatus* and the other species dealt with by him (*Athous subfuscus*, *Melanotus rufipes*, *Prosternon holosericeum*) feed chiefly on the nectar of flowers, though *P. holosericeum* eats the petals of *Cytisus*.

A number of different Elaterids in America and *Limonius minutus* in Russia (19) have been recorded as damaging fruit blossom, while *Adrastus limbatus*, Brit. Cat. (= *nitidulus*, Marsh) has been known to attack Strawberries (Carpenter (5)), but so far as *Agriotes obscurus*, *A. lineatus* and *A. sputator* are concerned, little is known of the nature of their food at large beyond the statement of Adrianov.

THE EGG.

The eggs of the four *Agriotes* species, *lineatus, obscurus, sputator* and *sobrinus* are laid in the soil at varying depths from a quarter of an inch down to two inches. Up to the time of going to press those of *A. lineatus* have not been procured at Rothamsted, but Adrianov obtained eggs of that species, together with *A. sputator*, in his breeding pots at depths of, approximately, $\frac{3}{4}$ to $1\frac{3}{4}$ inch, so that the site for oviposition in the four species named may be considered the same. Ova of *Athous haemorrhoidalis* have also been obtained from one of the breeding pots in a similar situation at a depth of $\frac{1}{4}$ to $\frac{1}{2}$ inch below the surface of the soil.

Adrianov found that eggs deposited too near the surface became desiccated and Graf (13) in America also found that those of *Limonius californicus*, Mannh. became desiccated when kept in a dry vial. Probably therefore the beetle descends into the soil for the purpose of obtaining a sufficiently moist nidus.

Oviposition takes place from towards the end of June to the middle of July. The ova have not been found in the open, but in the breeding pots in which the beetles have been confined from the end of May until their death, no ova have been discovered before the early days of July. From a comparison of the time of hatching of some of the ova with that of the maximum incubation period (which is about one month) it would appear nevertheless that some of the eggs are laid in June.

Ova of both *A. obscurus* and *A. sputator* have been found in burrows excavated by the beetles in the soil, in one case the burrow appearing to be more or less horizontal, in another vertical. It is possible that this may be commonly the case but the friability of the soil when it is examined renders it uncertain whether the burrow will remain intact. The friability of the soil also makes it difficult to say whether the eggs are always laid in clusters. Certainly this is frequently the case, 52 eggs of *A. obscurus* having been taken in close proximity, but many have also been taken singly and in twos and threes and these have almost certainly not always been detached from larger clusters. In the case of *A. sobrinus*, only a few eggs have yet been taken and no clusters were found, but in the cases of each of the other two species of *Agriotes* observed, as well as in that of *Athous haemorrhoidalis*, clusters of eggs have been found.

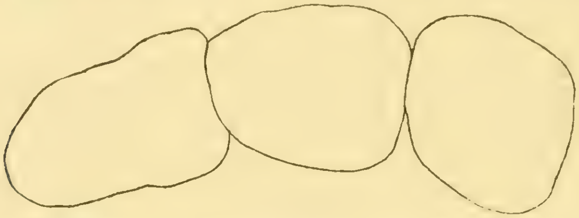


Fig. 1. Coherent ova of *Agriotes sobrinus*, Kies. Magn. × 50 approx.

The eggs in a cluster do not generally cohere at all fast, and no evidence has been forthcoming that they are in any real sense glued together, or to the soil in which they are laid, by any special material produced by the mother for the purpose, as is the case with some insects. Text-figure 1 is an outline drawing showing three eggs of *Agriotes sobrinus* which were coherent when dug up from the soil. One of them, which appeared to have cohered to the others in a plane at right angles to their long axes, eventually became detached under manipulation.

The actual environmental condition necessary for oviposition is a matter of the greatest practical importance and it is one which cannot at present be considered entirely solved. It seems from extrinsic evidence however to be probable that the presence of grasses, either cultivated or as weeds, is nearly, if not quite, an essential factor. Thus the typical situation in which wireworms are found in large numbers is grass-land, which has been laid down a considerable time. They may be present in arable land, but their number seems to bear a direct relationship to the state of cultivation of the land, making allowance for a ley of "seeds" or clover which will occur in the rotation.

It is concluded therefore that the eggs are laid about the roots of grasses and that such an environment is only provided by grass- or waste-land, a temporary ley (after which the wireworms found should be nearly of a size) or badly cultivated land on which couch or other grass weeds have been allowed to multiply.

The Larva.

No difficulty was experienced in hatching the young larvae, by allowing the ova to remain either on damp soil or moss. Possibly, however, there would have been trouble from desiccation, as Adrianov found, if care had not been used to supply a certain amount of moisture. The young larvae, when first hatched, at once make their way downwards into the soil and, as in the case of older larvae, appear to dislike a strong light. Except in pots where they have been known to be present, they have not been found in the soil and it is doubtful whether larvae, at least those of *lineatus*, *obscurus* or *sputator*, are ever found by farmers or gardeners in their first year of life. They are extremely small up to this age; they are pale in colour and possibly their food is not of quite the same nature as that of older larvae, so that there seems sufficient reason for their being overlooked.

Vassiliev (23) fed young larvae, up to a month or six weeks old, on rotten dung, while Adrianov found pieces of beetroot and carrot eaten to some extent and also found evidence of the larvae having eaten into the small roots of rye and wheat. In my own investigations young larvae have been kept for some weeks in tubes containing turfy soil and the gut, which is plainly visible through the cuticle, was found to be filled with a dark brown substance, evidently partially-decomposed vegetable matter. In the same way also larvae, kept in moss, have been found to have the gut filled with a green substance, the chlorophyll of the moss on which they had fed.

Some slight evidence of potato having been eaten was obtained, but it was not quite satisfactory and certainly larvae in the first instar have not been discovered boring tunnels into potato tubers in the manner of the older larvae. Tests made with growing barley at the end of the first, and during the second, instar afforded no positive evidence of damage. Ten larvae of *A. obscurus* were enclosed in a pot with plants just above the ground. At the end of six weeks, no evidence of attack could be found and the plants appeared in no wise inferior to those in the control pot. Possibly the smaller rootlets may have been attacked, but though the length of the larvae was doubled during the experiment, the plants appeared quite healthy.

The rate of growth of the young larvae in the first instar I have found to be exceedingly slow, differing in this respect from the experience of Adrianov. His specimens of *A. lineatus*, from a length of 1·25–1·75 mm. at hatching, had obtained a length of about 4·5–5·0 mm. in eleven weeks, while *A. sputator*, from 1·0–1·5 mm., had grown in a few cases to 6 mm. or even more. As he points out, however, the total number of specimens of the latter species examined was only small and he does not regard them as typical. Other tables for the two species, reared more nearly under field conditions, show *A. lineatus* on 25th September (? 7th October by Western Calendar) to be of an average length of 4·3 mm. and of *A. sputator* 3·5 mm.

As will be seen from the data given when dealing separately with the two species, larvae of *A. obscurus* and *A. sputator* were in general found to be larger than Adrianov's at the time of hatching (2–2·75 mm. for *A. obscurus*, 1–2·5 mm. for *A. sputator*), while *A. obscurus* barely attained to the length given by Adrianov for *A. sputator* in September—October of the year of hatching by the end of the first instar (in the following June).

Larval specimens of *A. sputator* from the 1916 brood have unfortunately been few in number, but so far as the information gathered from them goes, this species appears to keep pace with *A. obscurus* in rate of growth. At the end of twelve months, either species reaches little beyond the maximum length of Adrianov's laboratory-fed specimens of only eleven weeks' growth. Possibly *A. lineatus* may be of more rapid growth than *A. obscurus*, but the few laboratory-fed *sputator* of Adrianov which reached so great a length as 6 mm. must be regarded as quite exceptional; though even the average (3·5 mm.) of the large number (44) measured by him from his outdoor cultures considerably exceeded that of either *sputator* or *obscurus* in anything approaching a similar period at Rothamsted.

At the first ecdysis, which takes place in June, the larvae of *A. obscurus* had grown but little, but during the second instar their length was about doubled. The second ecdysis occurs at the end of July and in the beginning of August, so that growth at this point is rapid. After the second ecdysis the larva grows a little before the winter and then moults again about April or May of the following year. It is at this stage that the young larvae are generally first recognised in the field and they are then of a length of some 6·5–8·5 mm.

At the end of the second year of life, after two more ecdyses, the larvae have attained an average length of 10–11 mm., and are then very distinctly yellow. From this stage onwards observations have been made only on wild-caught larvae, but for *A. obscurus* it appears to be probable that the rate of growth is somewhat as follows:

3rd year from 11 mm. to 17–18 mm.
4th ,, ,, 18 ,, ,, 20–21 ,,
5th ,, ,, 21 ,, ,, 23–25 ,,

Such an estimate tallies with Bierkander's statement (Marsham (17)) that he had kept the larvae in confinement for five years. Ford ((11) p. 101) considers this period too long, but as will be noticed from his argument on the subject, he did not take into consideration the smallness of the larvae in the first year of life—the earliest stage known to him being larvae of 7 mm. in length—nor the fact that growth in the last year is very small. The figures given above are approximate only but are taken from data of measurements of wild-caught larvae together with laboratory observations on their subsequent development.

The fact does not appear to have been generally recognised that the larvae normally moult twice in the year, in April and May and again between July and September. It appears to be true both for *A. obscurus* and *A. sputator*; also for some other species of Elaterid larvae. The summer moult is the most noticeable, since all the larvae appear to be at ecdysis at nearly the same time. At this time the larvae under natural conditions are deep in the soil, possibly as a protection from the appetites of those few which are not in the same condition and of other predaceous insects. The spring moult does not appear to take place amongst all the larvae at one time to the same extent, but there is no doubt about its occurrence. A number of cases have been noted among laboratory-fed larvae; but in addition exuviae, evidently freshly shed, have been found out-of-doors in April and larvae brought into the laboratory from outside in May have moulted within a short time afterwards. Graf (13) found the same in the case of *Limonius californicus*, an American pest of sugar-beet, but he records it in rather a tentative manner (p. 30), though evidently expecting that subsequent experience will confirm the results which he obtained in 1912.

Evidence has also been obtained that the larvae of *Athous haemorrhoidalis, Corymbites cupreus* and others which are believed to be *C. pectinicornis*, L., undergo two ecdyses in the course of the year, but this cannot yet be certainly stated.

Agriotes larvae will feed upon almost any crop and apparently upon a good many weeds, apart from grasses, which were probably their original food-plants. They are not however indifferent to the species of plant which they attack and though mustard does not appear to be absolutely immune, as was once supposed, it is probably only attacked in the absence of some more palatable plant. Charlock on the other hand appears to be favoured, larvae having been found boring into the root in cornfields, where it might be supposed their choice would be exercised otherwise. Beans usually do not suffer so much as other crops, but wireworms will on occasion attack the seed beans in the ground. Attacks in pots are difficult to induce, but in a test on a small scale, one bean out of four sown was found somewhat eaten, there having been ten wireworms in the pot. The other three beans were not affected and all four plants subsequently developed equally well.

Potatoes are often much damaged by *Agriotes* larvae and to some extent also by *Athous haemorrhoidalis*, but much of the damage done to potatoes and attributed to wireworms is in reality wrought by slugs and millipedes. *Athous haemorrhoidalis*, and also *Agriotes*, have been reported as pests of tomatoes grown in glass-houses (Carpenter(6)), the latter of course being a well-known trouble to the grower. The larvae enter the plants below the ground-level and, boring their way up the stem, kill the plants, frequently at a time when it is too late in the season to replace them. The fondness of *Agriotes* for the roots of Dock (Rumex) has been noted by Curtis ((7) p. 159) and both it and *Athous haemorrhoidalis* have been found in or about them.

It is hardly necessary to mention the propensity of *Agriotes* for attacking young growing corn, but we do not appear to suffer seriously in this country from attacks on the sown seed, though experimentally larvae have been found to hollow out corn seed in the laboratory. In the United States and other parts of America the attacks of *Agriotes* and other genera on seed is serious and they are also stated to be injurious to maize seed in Russia (Vassiliev(24)). Probably in this country the seed of cereals is sown too late in the autumn and too early in the spring to be much affected by wireworm attack before the plant develops.

Apart from the capacity of the larvae for fasting, there is no doubt that they can subsist in any ordinary soil for a very lengthy period with no food other than humus and decaying vegetable matter. Graf(13) records an experiment made by H. M. Russell on *Limonius californicus* to test the capacity of the larvae for subsisting, as he supposed, without food. "Ordinary soil" alone was given, and, for the first thirteen months of the experiment, it was regularly watered. At the end of this time seven larvae were alive and healthy. The soil was then allowed to become dry for some two months and during this time all the larvae died except one, their bodies being removed as they died from desiccation, to prevent them from being used as a source of food by the survivors. Watering was then resumed and the one survivor continued to live until it died through an accident twenty months after the commencement of the experiment. This treatment was not of course in any sense normal to the larvae and the species dealt with of a different genus from any of our native species known to be injurious. Nevertheless the experiment throws light on the capacity of "wireworms" to withstand starvation by fallowing, *per se*, or by the use of mustard as a "starvation crop" on infested land. I have made no experiment lasting over so long a period, but from observations made in the laboratory and in pot cultures, there can be little doubt that *Agriotes* larvae would succeed in maintaining life in similar conditions for a very considerable time, if not actually for so long as *Limonius californicus*. Larvae have been kept for some months on a diet of vegetable compost during the spring and summer and in the laboratory have frequently been kept in boxes for prolonged periods with no food other than decaying roots and the humus contained in the soil. They do not thrive under such a treatment as the last named, but life is maintained and it is certain that nourishment is derived from the organic matter contained in the soil. On the other hand, provided that sufficient moisture is supplied, *Agriotes* larvae (and those of other Elaterids) are able to fast for a considerable time without apparent inconvenience. In order to test this, three larvae of different sizes were isolated in wide glass tubes containing only moistened sand which had been previously sifted and treated with acid. One larva was able to reach the cork of its tube and was found gnawing it about a week after the commencement of the experiment. At the end of one month all the larvae were found to be alive and active, having apparently suffered no ill effects from the treatment. It should be added that the experiment took place in February and March, so that there was probably no excessive reserve of fat in the bodies of the larvae such as might have been the case at the end of summer.

In the course of experiments to test the toxicity of certain substances as insecticides, several instances of the power of the larvae to withstand starvation have also been noted. In one case, the larva was evidently affected by the insecticide, which was not of a concentration sufficient to kill it. Treated on the 21st June it still remained, three months later, in much the same condition as immediately after treatment. It was supplied with pieces of potato, but these were not eaten and eventually the larva died—whether from the effect of the insecticide or from starvation could not be ascertained.

Larval *Agriotes* can withstand immersion in water for a very long time. In glazed pots which have remained filled with rainwater for at least a few days, they have afterwards been found alive. Bierkander (17) found they could live in water for four days, but Del Guercio (8) found that death only took place after twenty to thirty days' submersion and that, as he points out, at a time (June—July) when metabolism may be considered at its height.

Graf ((13) at p. 27) notes that some of the beet fields which have suffered the most from the attacks of *Limonius californicus* are those which almost every year are quite thoroughly flooded for two or three days. It appears therefore that irrigation for any reasonable period is hardly likely to have any controlling effect.

It has been stated by Del Guercio (8) that the larvae (of *A. lineatus* and *A. obscurus*) feed during the winter between October and March, on decaying vegetable matter and it is probable that such is often the case. When grass-land has been newly ploughed, wireworms may be found, in winter, still in the sod at or quite near the surface, even in hard weather, provided that the sod remains sufficiently damp. They have also been found repeatedly in winter, when digging in the sod heaps mentioned above or on grass-land, amongst the roots of grasses growing on the surface, even during the continuance of frost and snow. Such larvae may be contracted and sluggish at the time, but appear to suffer no permanent damage and revive quickly when brought under milder conditions. At the same time that these larvae are found near the surface on grass-land, others may be found at considerable depths below. Thus, for example, in a hole dug to a depth of 31 inches in one of the sod heaps at the end of December, 1917, 14 *Agriotes* larvae were taken. Of these nearly half were taken amongst the roots of plants growing on the surface or in the first spit (9 inches) of soil, but the remainder were found lower, at depths from the surface of 14 down to 24 inches.

In the case of arable land, which has not been recently ploughed out of grass, the larvae are not found near the surface in winter, unless perhaps in very mild weather. In a series of tests made in a field known to be infested, none were found nearer the surface than six inches, while several were found in the subsoil, which in this field was at some 10–12 inches from the surface. It is possible that larvae at such a depth might move in their burrows nearer to the surface through the influence of rain and mild weather, but it seems likely that little food, if any, would be taken between the time when they went deep into the soil and that when they returned to feed at the surface in spring. Probably therefore in many cases we have a condition of hibernation similar to that obtaining with many lepidopterous and other larvae, though in others the larvae remain in the sod at or near the surface, feeding on the roots.

As mentioned above, the larvae in the course of their movements through the soil construct burrows, so that in case of necessity they are able to retreat fairly rapidly. These burrows impress the observer when a large number of larvae are kept together in the confined space of a pot and the soil is of such a character that they remain undamaged, when it is lifted out in blocks. The burrows are then seen to honeycomb the soil, ramifying up and down and in all directions.

In the burrow the larva changes its skin, sometimes enlarging the burrow in the process to form a similar cell to that in which pupation takes place. Such cells are also frequently formed for hibernation and the larvae in a sluggish condition may be found in them in winter.

Mention must also be made of the propensity of *Agriotes* larvae for animal food alive or dead. Probably in nature little opportunity occurs to most larvae to indulge their tastes in this direction, but in captivity, as is well known, they will readily feed upon one another, even in the presence of vegetable food. Except in case of injury or at the time of ecdysis, the thick chitin of the cuticle is usually sufficient protection. At ecdysis however the larva is helpless both before and immediately after the moult takes place, so that in the case of larvae kept in a confined space the mortality is very great.

PUPAL STAGE.

Pupation takes place in the ground, within a cell prepared beforehand by the larva. So far as my observations extend, the pupa is placed erect in the cell, with the head uppermost. This habit has also been observed by Hyslop (16) in the case of the American species *Agriotes mancus*, Say.

The pupal instar extends over a period of about three weeks, while pupae have been found from the latter end of July up to the middle of September.

It is often stated, for instance by Miss Ormerod (18), that the larva descends for a considerable distance beneath the surface to pupate. Reh (20) however says that it pupates close to the surface ("in geringer Tiefe") up to a depth of 10–15 cm. This also has been my experience, principally with *A. obscurus*, the following being records from my note book of two tests made by digging in the sod heaps at Windermere, each to a depth of one foot.

5. viii. 18.	2	pupae	at	1″	from	surface	6. viii. 18.	1	pupa	at	1″	from	surface
	1	pupa	,,	2″	,,	,,		2	pupae	,,	1–2″	,,	,,
	1	,,	,,	less 3″	,,	,,		1	pupa	,,	2″	,,	,,
	1	,,	,,	3″	,,	,,		1	,,	,,	3″	,,	,,
	1	,,	,,	4″	,,	,,		2	pupae	,,	less 4″	,,	,,
	1	,,	,,	7½″	,,	,,		1	pupa	,,	4″	,,	,,

Larvae pupating in pots at Rothamsted were similarly found in some cases quite near the surface and though they are found to a much greater depth than those mentioned, the habit of pupating deep in the soil, beyond the depth of a plough, is by no means universal.

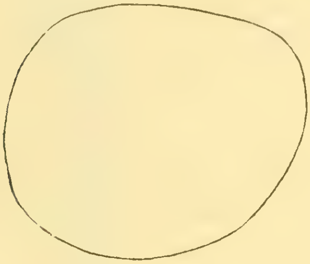
NATURAL ENEMIES.

This subject has been so thoroughly dealt with in the paper by Ford (11) already quoted, that there is but little to add. In confirmation of the value of birds in reducing the number of "wireworms," reference may be made to the work of Miss Laura Florence at Aberdeen (10) especially in regard to the quantity consumed by other gulls than the black-headed gull, which has been well-known as an ally of man in this respect. Hammond's work (14) on the food of birds in the Eastern Counties of England is also of great value, bringing out, amongst other points, the fact that the skylark is of assistance in the control of these pests. Berry (3) found many wireworms in the crops of pheasants in Scotland, but Evershed and Warburton (9) appear to have found but few. Probably local and temporary conditions account for the difference.

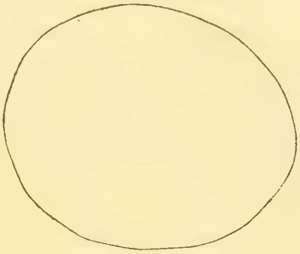
There is no doubt that birds are one of the most important factors in the natural control of wireworms and it is probable that under conditions where such a course is possible, their numbers might be appreciably reduced if poultry, especially those of good foraging strains, were run for a time on land newly ploughed out of grass.

Wireworms do not appear to be attacked by internal parasites to any great extent. Marsham (17) records that Bierkander found six out of thirty wireworms parasitised by an ichneumon (possibly a Proctotrupid) and Mr Fryer, as noted by Ford, has obtained Proctotrupids from *Agriotes* larvae.

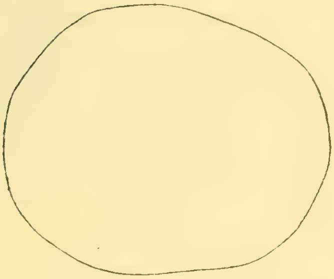
In June, 1916, there emerged eleven larvae of a Proctotrupid from a larval *Athous haemorrhoidalis* taken at Windermere in the preceding April. A few days later the larvae were found to have pupated with their heads distal to the body of the host and the eyes showing dark through the creamy white integument. At this stage they resembled the figure given by Sharp (21) of pupal Proctotrupids, parasitic on an unknown beetle larva. On July 9th nine imagines emerged, one larva having been killed and one pupa having died without emerging. Five of the imagines were submitted to Mr James Waterston, of the Imperial Bureau of Entomology, who, with Dr R. C. L. Perkins, examined them and reported that all were females of a species of the genus *Phaenoserphus* (Kieff., 1908), probably *P. fuscipes* (Haliday, 1839). To these



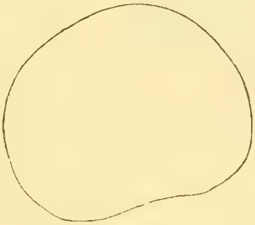
2



3



4



5

Fig. 2. *Agriotes sobrinus*, Kies.: ovum. Magn. × 75 approx.
Fig. 3. *Agriotes sputator*, L.: ovum. Magn. × 75 approx.
Fig. 4. *Agriotes obscurus*, L.: ovum. Magn. × 75 approx.
Fig. 5. *Athous haemorrhoidalis*, F.: ovum. Magn. × 75 approx.

two gentlemen my thanks must be expressed for their careful examination.

The only other case of parasitism by an insect occurred in the case of a larval *Agriotes obscurus*, probably also from Windermere, handed over to Dr Malcolm Laurie, of this station, for examination of the internal anatomy. Within the larva he found several larval parasites, which he believes are also referable to the family *Proctotrupidae*.

Wireworms are apparently parasitised by a fungus of the genus *Isaria*, as has been already stated in the Board of Agriculture leaflet (4). Critical work on the subject is necessary to be certain that the fungus is not in reality a saprophyte, though from my experience with it there is a strong presumption that it is truly parasitic.

In one of the sod heaps previously mentioned portions of larval *Agriotes* have been found on one or two occasions, consisting of a thin layer of external chitin only, the whole of the interior portions of the larvae being represented by a mass of fungus hyphae. Similar cases have occurred amongst laboratory-fed larvae obtained from the same source and the fungus has been induced to grow upon apparently healthy larvae by enclosing them in a box with an affected larva, upon portions of which they fed. Fig. 3 (Plate IV) represents the fungus growing from a specimen of *Agriotes obscurus*. The photograph was taken by Mr W. F. Bewley, to whom and to Mr W. B. Brierley I am greatly indebted for assistance and advice in dealing with this branch of our subject.

REFERENCES.

(1) ADRIANOV, A. P. *Report on the work of the Entomological Bureau* (of Kaluga) *in* 1913–14. Kaluga, 1914. Brief abstract in *Review of Applied Entomology*, series A, III (1915), 309.

(2) BELING, TH. Beitrag zur Metamorphose der Kaferfamilie der Elateriden. *Deutsche ent. Zeits.* XXVII (1883), 138.

(3) BERRY, W. *Scottish Naturalist*, No. 66 (1917), 121–135. Abstract in *Rev. App. Ent.* A, V (1917), 348.

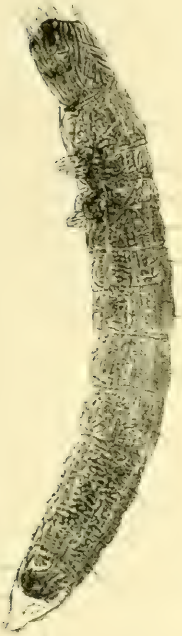
(4) Board of Agriculture. *Leaflet* No. 10, 1918.

(5) CARPENTER, G. H. Report on Injurious Insects in Ireland in 1905. *Econ. Proc. R. Dublin Soc.* I, 339.

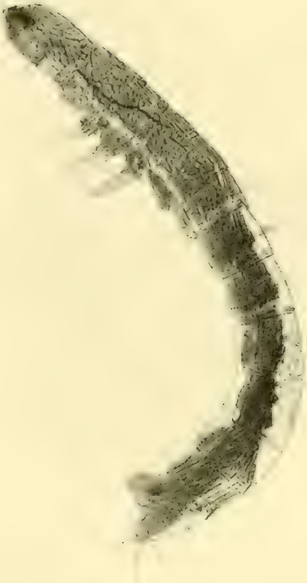
(6) —— Report on Injurious Insects in Ireland in 1910. *Econ. Proc. R. Dubin Soc.* II, 49.

(7) CURTIS, JOHN. *Farm Insects*, 1860.

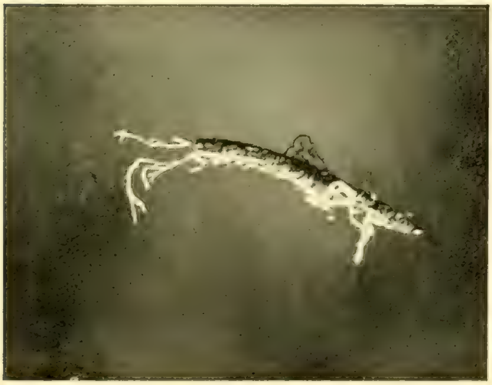
(8) DEL GUERCIO, G. Prima contribuzione alla conoscenza degli Elateridi, etc. *Redia*, VI (1910), 235–241.



1



2



3

(9) Evershed, A. F. C. H. and Warburton, C. Pheasants and Agriculture. *Jour. Agric. Sci.* IX (1918), 63.

(10) Florence, Laura. "The Food of Birds." *Trans. Highl. and Agric. Soc.* vols. XXIV, XXVI, XXVII (1912, 1914, 1915).

(11) Ford, G. H. Observations on the larval and pupal stages of *Agriotes obscurus*, L. *Ann. App. Biol.* III (1917), 97–115.

(12) Fowler, W. W. *Coleoptera of the British Islands*, vol. IV, pp. 101, 107–109.

(13) Graf, J. E. A preliminary report on the Sugar-beet Wireworm. *U.S. Dept. Agric. Bur. Ent. Bull.* (1914), 123.

(14) Hammond, J. An Investigation concerning the food of certain birds. *Jour. Agric. Sci.* IV (1912), 386.

(15) Henriksen, K. L. Oversigt over de danske Elateride larver. *Ent. Meddel.* IV (1911), 225–331.

(16) Hyslop, J. A. Wireworms attacking cereal and forage crops. *U.S. Dept. Agric. Bull.* 156, 1915.

(17) Marsham, T. *Communications to the Board of Agriculture*, IV (1805), pp. 412–415 (Records Bierkander's investigations).

(18) Ormerod, E. A. *Manual of Injurious Insects*, 2nd ed. (1890), p. 110.

(19) Petrograd: (Report of) Central Phytopathological Station, 1913. Abstract in *Rev. App. Ent.* A, III (1915), 223.

(20) Reh, L. Handbuch der Pflanzenkrankheiten von Prof. Dr P. Sorauer. Dritter Band (1913), 481.

(21) Sharp, David. *Camb. Nat. History*, vol. v, p. 535.

(22) Sharp, W. E. *Coleoptera of Lancashire and Cheshire*, p. 53, 1908.

(23) Vassiliev, E. M. Report to All-Russian Soc. of Sugar Refiners in 1913. Kiev, 1914. Abstract in *Rev. App. Ent.* A, II (1914), 466.

(24) —— *South Russian Agric. Gazette*, Charkov, 1914. Abstract in *Rev. App. Ent.* A, III (1915), 541.

(25) Westwood, J. O. *Introduction to the Classification of Insects*, I, p. 237, 1839.

EXPLANATION OF PLATE IV

Figs. 1 and 2. *Agriotes obscurus*, L. Larvae in 1st instar: about six weeks old. Magn. × 40 approx.

[*Photos. by Flatters & Garnett, Ltd.*

Fig. 3. Larva of *Agriotes obscurus* attacked by *Isaria* sp.

[*Photo. by W. F. Bewley.*

ON A COENURUS IN THE RAT.

By M. TURNER, B.Sc.

(*Helminthological Department, London School of Tropical Medicine.*)

(With 1 Text-figure.)

The Rat plays so important a part in economic life and welfare of all peoples that, for many years, it has been the subject of minute and routine examinations. Because of this, its parasites are well-known and have been described in several important monographs. In 1908, Dr A. E. Shipley, Master of Christ's College, Cambridge took "Rats and their Animal Parasites" as the subject of his Presidential Address to the Association of Economic Biologists, and the same theme formed a considerable part of the Presidential Address of Dr Burton Cleland to the Royal Society of New South Wales in 1918.

One of the most common parasites of the rat is the larval tapeworm, *Cysticercus fasciolaris*, which infests the liver. Owing to the atypical appearance of this larval tapeworm it is frequently received by the Helminthological Department of the London School of Tropical Medicine for special diagnosis. With a similar object Dr W. M. Graham some years ago forwarded a collection of parasitic worms, made during a routine examination of rats at Accra, in connection with an outbreak of plague on the Gold Coast. The collection included several specimens of *Cysticercus fasciolaris*, and also a large ellipsoidal cyst which had been found in the abdomen of a rat. More recently Dr J. A. Murray, Director of the Imperial Cancer Research Laboratories, kindly sent two tapeworm cysts which came under his notice while examining mice purchased in London. Through the courtesy of Professor Leiper I was able to investigate all three cysts in detail.

The usual form of a larval tapeworm is the Cysticercus, which is a bladder-like cyst that bears on its internal surface one bud. In the definitive host this bud develops into the head of the adult worm. The cysts found in the rat and mice agree with the Cysticercus in having a vesicular shape but differ from it in having numerous buds instead of only one. For this reason the three cysts from the rat and mice belong to the group of polycephalous larval tapeworms known as "Coenurus."

No Coenurus has been recorded in either the rat or mouse before, though they have been found in other members of the group Muridae. In the Jerboa is *Coenurus polytuberculosus*, Megnin, 1880, and in the Gerbille, *Coenurus glomeratus*, Railliet et Henry, 1915.

Unfortunately the cysts from the mice are very immature, the buds having not yet developed hooks or suckers so that it is impossible to compare them with other forms of Coenurus.

Besides these from the members of the Muridae, the group Coenurus contains five more species, viz. *C. cerebralis* of sheep, *C. gaigeri* of goats, *C. serialis* of rabbits, *C. ramosus* of Macacus sinicus and *C. lemuris* of lemurs. Of these *C. cerebralis* and *C. serialis* most nearly resemble that from the rat.

Examination of the scolices of the rat Coenurus, of *C. serialis*, of *C. cerebralis* and of *C. glomeratus* has revealed the fact that there is a considerable amount of variation amongst the individual hooks. Hooks from the same scolex vary in length and shape within fairly wide limits, so that it is in some cases difficult to distinguish between two species when the material for diagnosis consists solely of a limited number of hooks.

Coenurus from the Rat.

The entire cyst is ellipsoidal in shape and measures about 2 cm. in length by 1 cm. in breadth. The cyst-wall is thin, and transparent enough to allow the buds, which cover almost the whole of the inner surface of the wall, to be clearly seen. About twenty buds project from the outer surface of the cyst. Each head, in both lateral and face view, is approximately circular in shape, with a diameter of about 650μ.

The suckers are of fairly large size. Their muscular bulbs have diameters of about 230μ. The rostellum is about 330μ in diameter and bears a double crown of from 24 to 28 hooks.

The large hooks are from 130μ to 145μ in length and the blade, handle and guard are all well developed.

The blade is moderately curved.

The handle is long and straight and very slightly tapering. Its dorsal and ventral margins are practically parallel and somewhat sinuous. A notch is sometimes present on the dorsal margin about the middle of the handle. The free end of the handle turns dorsally.

A line drawn transversely through the centre of the guard shows that the handle is considerably longer than the blade. This gives the handle a slender appearance.

The guard of the large hook is triangular in shape in lateral view, with its maximum diameter at the base. The free end of the guard is usually pointed.

The small hooks are from 90μ to 105μ in length. The blade is moderately to well curved.

The handle is quite thick and long. It is very slightly tapering at the distal extremity, is bent somewhat dorsally, and its axis meets that of the guard at an angle of from 100° to 110°.

The face view of the guards of both large and small hooks is broad, though the guard of the small hook is wider than that of the large hook. Each of these guards has tapering edges and a median groove but is not bifid.

The hooks of the *Coenurus of the rat*, of *Coenurus cerebralis*, and of *Coenurus serialis*, appear to be formed after the same type. Both the large and the small hooks are about the same size in all. The small hooks of the Coenurus of the rat and *Coenurus cerebralis* are much alike in their chief features, but that of *Coenurus serialis* differs rather markedly from these in the character of the handle. In the large hooks of all, the handle, blade and guard are well developed. In all the handle is straight in its general direction. The blades of all the large hooks are moderately curved. Nevertheless more detailed examination of my material showed that the hooks, both large and small, of each Coenurus possess some features in which they differ from the hooks of any other Coenurus, though in some cases the difference may be only one of degree.

In the material examined which consisted of one cyst from the rat, one cyst of *C. cerebralis*, and two cysts of *C. serialis*, each scolex of the Coenurus from the rat bears 24 to 28 hooks. Each of three scolices of *Coenurus cerebralis* bears 26 hooks, while each scolex of *Coenurus serialis* bears from 26 to 30 hooks. Hall, 1919, says that a scolex of *Coenurus cerebralis* bears from 22 to 32 hooks, and one of *Coenurus serialis* bears from 26 to 32. Thus the number of hooks in each scolex is about the same in the three Coenurus; viz. the Coenurus from the rat, *C. cerebralis*, and *C. serialis*.

The large hooks of the Coenurus from the rat are from 130μ to 145μ in length; those of *C. cerebralis* from 145μ to 165μ and those of *C. serialis* from 135μ to 145μ. So that here the large hooks of *C. cerebralis* are longer than those of the Coenurus of the rat and *C. serialis*. Hall gives the length of the large hooks of *C. cerebralis* as from 150μ to 170μ and the length of those of *C. serialis* as from 135μ to 175μ. In this case some of the hooks of *C. serialis* are longer than those of *C. cerebralis*.

The blade is of moderate curvature in all the large hooks. The axis of the handle in the Coenurus of the rat, in *C. cerebralis* and in *C. serialis* is straight. In all the dorsal and ventral margins of the handle are practically parallel and somewhat sinuous. The curves of these margins are large in *C. serialis*, and very slight in the Coenurus of the rat.

The handles of the large hooks of the Coenurus of the rat, of *C. cerebralis* and of *C. serialis*, all taper distally, but very slightly so in the two first and more so in the last. In all the distal end of the handle of the large hooks tends to turn dorsally. In *C. cerebralis* this dorsal bend is usually scarcely perceptible; in *C. serialis* it is more pronounced, while in the Coenurus of the rat, it is very marked in many of the hooks.

The proportion of the height of the blade to the length of the handle in the large hooks of one Coenurus is not the same as that of the hooks of another Coenurus. In all the large hooks from the Coenurus of the rat the handle is noticeably longer than the blade, which gives the handle a slender appearance. In *C. serialis* the handle may be somewhat longer than the blade though usually they are about equal. In *C. cerebralis* the blade is longer than the handle so that the handle appears strong and thick.

A notch is frequently present on the dorsal margin of the handle of the large hook of *C. cerebralis* and is often seen in some hooks of the Coenurus of the rat.

One of the chief features by which these large hooks may be distinguished is the shape in lateral view of the guards. In the hooks of the Coenurus of the rat the guard is triangular with its maximum diameter at the base and usually with a pointed distal end. The guard of *C. cerebralis* is practically cylindrical for some way out from its base and then tapers sharply to its free extremity. Its greatest diameter is usually just before the guard begins to taper.

In the majority of the large hooks of *C. serialis* the guard is almost cylindrical with a blunt rounded tip.

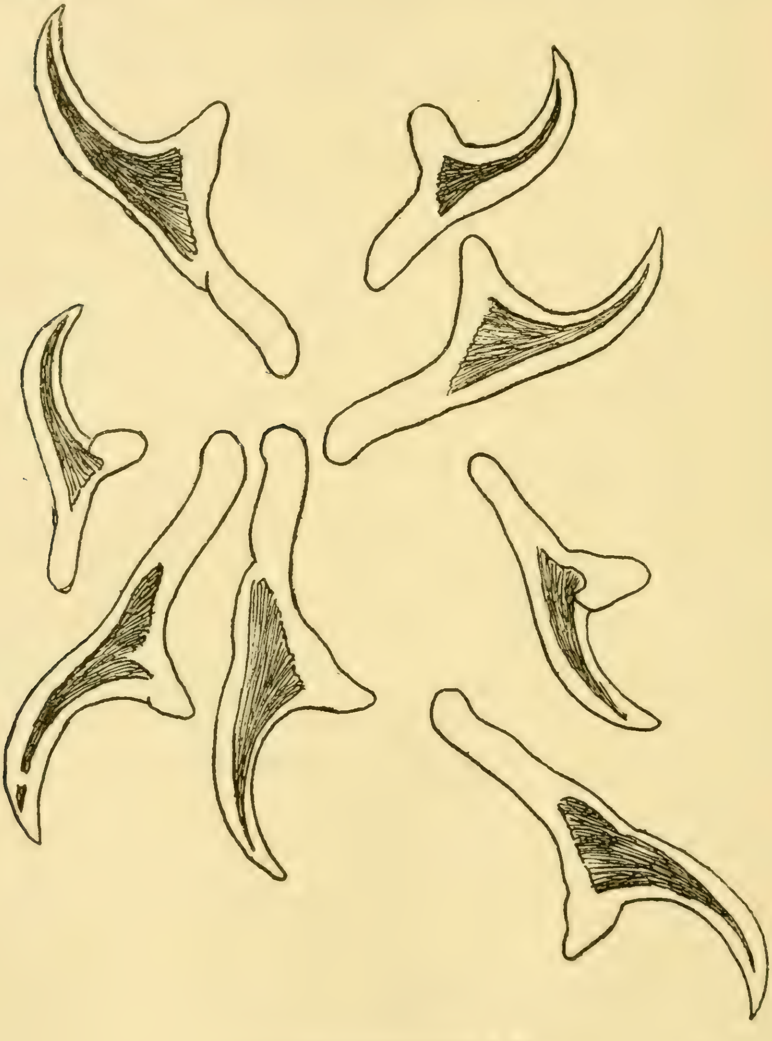
In *C. cerebralis* and *C. serialis* the core of the hook does not enter the guard but in the hooks of the Coenurus of the rat it penetrates the broad base of the guard for a short way.

The axes of the guard and the handle of the large hooks of each Coenurus meet at about 90°.

In my material the small hooks of the Coenurus from the rat are from 90μ to 105μ in length: those of *C. cerebralis* are from 95μ to 120μ (Hall gives 90μ to 130μ) and those of *C. serialis* from 90μ to 100μ (Hall gives 78μ to 120μ). So that the small hooks of *C. cerebralis* are the longest.

The curve of the blade of the small hook of each Coenurus is from moderate to strong.

The guard is well developed in all three small hooks. Their shape in each Coenurus is not so constant as that of the guards of large hooks. Yet the guard of the small hook of the Coenurus from the rat is usually almost cylindrical with a rounded tip. In the small hooks of *C. cerebralis* the guard is usually long and tapering, while in those of *C. serialis* it is



Hooks of a Coenurus from a rat.

usually short and rounded. The face view of the guards of all the hooks of the Coenurus from the rat, of *C. cerebralis* and *C. serialis*, is broad, and in all it is wider in the small hooks than in the large.

The small hooks of the Coenurus from the rat and of *C. cerebralis* have quite long handles, which are tapering in both but those of *C. cerebralis* are more so than those of the Coenurus from the rat. The handles of the small hooks of *C. serialis* are usually short. In the small hook of the Coenurus from the rat and in *C. cerebralis* the axes of the guard and handle meet at an angle of from 100°–110°. In *C. serialis* this angle is from 130°–140°. All the handles bend somewhat dorsally, but as these figures show, that of the small hook of *C. serialis* is much more curved than those of either of the small hooks of the Coenurus of the rat or of the small hooks of *C. cerebralis*.

The differences in the hooks of the Coenurus of the rat of *C. cerebralis* and of *C. serialis* that have been given above are true for the great majority of hooks. Yet, as has been mentioned, variation amongst the hooks sometimes obscures their distinguishing features. For example several small hooks of *C. cerebralis* have been found with short dorsally curving handles, so that if they had been isolated when examined they would have been diagnosed as small hooks of *C. serialis* as in this Coenurus the majority of small hooks have dorsally curving handles.

In my material the tissue of the cyst from the rat and of that of *C. cerebralis* contained numerous calcareous bodies, but they were absent in both cysts of *C. serialis*. Hall says that in his examples of adult *Taenia serialis* the calcareous bodies were extremely abundant.

From the data given above it is evident that the Coenurus from the rat is either a new species or a very atypical form of a known species. A more definite conclusion than this is impossible owing to the scantiness of necessary material.

REFERENCES.

(1) Burton Cleland, J. (1918). Presidential Address to the Royal Society of N. S. Wales, Sydney, May 1st, 1918. Issued Sept. 5th, 1918.

(2) Hall, M. C. (1919). The Adult Taenioid Cestodes of Dogs and Cats, and of Related Carnivores in North America. *Proc. of the United States National Museum*, vol. LV, pp. 1–94.

(3) Megnin, J. P. (1880). Sur une Nouvelle Forme de Ver Vésiculaire. *Jour. de l'Anat. et Physiol.* etc., Paris, vol. XVI (2), 26 mars. 1880.

(4) Railliet et Henry (1915). On Coenurus glomeratus in the Gerbille. *Bulletin de Path. Exotique,* 1915, vol. VIII.

(5) Shipley, A. E. (1908). Rats and their Animal Parasites. *The Journal of Economic Biology,* vol. III, part 3, 1908.

SOME FACTORS IN PLANT COMPETITION.

By WINIFRED E. BRENCHLEY, D.Sc.

(*Rothamsted Experimental Station.*)

(With 10 Text-figures and Plate V.)

One of the commonplaces of agriculture and horticulture is that when plants of the same or different species grow in juxtaposition a mutual influence is exerted which is known as "competition." Every plant needs a certain definite supply of such essentials as food, water and light to enable it to reach its full development, and when other individuals with similar requirements are in the near neighbourhood they encroach upon these supplies and a sharp struggle for existence is the outcome. This fact of competition is fully recognised by every practical man, and much nicety of judgment is often exercised to give a crop adequate room for reasonable development in order to obtain the largest yield possible from a given area of land. It is not always an economic policy to give each plant the space it needs to attain its maximum growth, as the individuals may benefit at the expense of the total crop. Under certain circumstances, however, this policy of eliminating competition as far as possible is markedly successful, as in the case of wheat growing in the droughty districts of China[1]. The wheat is planted in "hills" arranged in double rows spaced widely apart, the hills being 24 to 26 inches from centre to centre, the rows 16 inches apart, and the space between each pair of rows 30 inches. In an unusually dry season a yield of 12 bushels per acre is obtained by this method, whereas in a very favourable season (as 1901) as much as 116 bushels[2] has been reported for small areas. Without this very specialised method of cultivation in these districts it would be impossible to obtain a wheat crop at all, but in most places with larger rainfall the end would not justify the means. A good many experiments have been carried out on thick versus thin seeding of cereals, wide versus narrow drills, etc., the results varying with locality and season. It is, however, generally recognised that up to a certain point it is profitable to give growing crops plenty of room, but that beyond this limit the total yield is apt to fall off.

---

[1] King, F. H., *Farmers of Forty Centuries*, pp. 239–242.

[2] There is no evidence to show the weight per bushel in this case.

Up to the present time most of our knowledge of competition has been purely empirical and derived from observation and deduction from plants grown under various cultural conditions not under strict control. Consequently little information is available as to the relative importance of the different factors that come into play when one plant enters into competition with another, or of the interaction between these factors. During the past five years a number of experiments have been carried out at Rothamsted which aimed at isolating some of the more important of these factors, and establishing their relationship to the growth of the plant. A full discussion of the problem will not be possible till far more data have been accumulated, but a preliminary account will indicate the present position of the work.

"Competition" of one plant with another is a very complex, not a simple, phenomenon, and may be broadly analysed as follows:

(1) Competition for food from the soil.
(2) Competition for water.
(3) Competition for light.
(4) The possible harmful effect due to toxic excretions from the roots, if such occur.

The first three factors lend themselves to direct experiment; the fourth is more difficult to demonstrate but the possibility of its existence must be reckoned with in estimating results.

1. GENERAL COMPETITION.

(*Including* 1, 2, 3 *above at the same time.*)

Pot cultures were carried out with mustard and barley, glazed earthenware pots being used, each holding 10 or 20 kilos of soil. The soil was obtained from an unmanured area on Great Knott Field, Rothamsted, sifted, and mixed with 10 per cent. sand to lighten it before use. No manures were added in any case, so that the only mineral food available for the plants was that present in the soil at the beginning of the experiment. The seeds were sown in double quantity, but as soon as germination was established the seedlings were thinned out to the correct number per pot. All seedlings thus removed and any weeds that put in an appearance were laid on the surface of the soil in order to avoid removing any of the original food supply and so altering the balance between the pots. Watering was done regularly, a similar quantity being given to every pot on each occasion, so that the amount of water available during the progress of the experiment was the same in every case.

Varying degrees of competition were induced by variations in the rate of seeding, from one to five plants being raised in the narrow pots containing 10 kilos of soil, and from one to eight in the broad pots with 20 kilos of soil. The pots were arranged in groups of five or eight (one pot of each rate of seeding per group) and the groups were scattered over the glasshouse on trucks to equalise conditions. When growth was well established and the weather was favourable the trucks were run outdoors into a wire cage. Mustard and barley were both tested, 10 narrow pots or 3 broad pots being used as a unit in every case.

EXPERIMENT I.

Mustard.

Narrow pots, 10 kilos soil.
Seeds sown March 31st, 1917. One to five per pot after initial thinning.
Plants cut May 29th, 1917.

Very soon after the plants had emerged from the seedling stage it was evident that the strength of development was in inverse ratio to the number of plants per pot, and this relation became more and more marked as time went on. The mustard was cut while most of the plants were in full flower, though some had begun to go over into fruit. A definite gradation of maturity occurred according to the number of plants in the pot. The *single plants* (per pot) were very strong, sappy, exceedingly tall and decidedly less mature than any others. The lower leaves had begun to turn yellow but were not at all wilted and none had dropped off. In most cases only the lowest flowers were fully developed, the upper ones being in various stages of bud, while the axillary racemes had hardly any flowers open. The *five plants per pot* were of medium strength only, comparatively short, with stems inclined to be woody, and were the most mature of all. The lower leaves had wilted and in many cases had dropped off, so that they had to be gathered up for the purpose of weighing. The flowers were fully out, and many on the main stem had begun to form fruit.

The 2, 3, 4 plants per pot showed a steady gradation between the two extremes of 1 and 5 plants per pot.

Table I.

Average results per pot (average of 10 pots).

No. of plants	Green wt. gm.	Dry wt. gm.	% dry in green	Water present gm.	% N in dry	Actual N gm.
1	44·40 ± 1·12	7·88 ± ·22	17·93 ± ·64	36·52 ± ·9	1·84	·144 ± ·004
2	43·05 ± 1·54	8·24 ± ·26	19·30 ± ·54	34·81 ± 1·28	1·77	·145 ± ·005
3	42·03 ± 0·90	8·69 ± ·13	20·83 ± ·42	33·34 ± ·77	1·66	·144 ± ·003
4	36·55 ± 0·91	8·17 ± ·36	22·32 ± ·26	28·38 ± ·55	1·62	·132 ± ·005
5	39·08 ± 1·07	8·53 ± ·18	21·92 ± ·31	30·55 ± ·89	1·57	·134 ± ·005

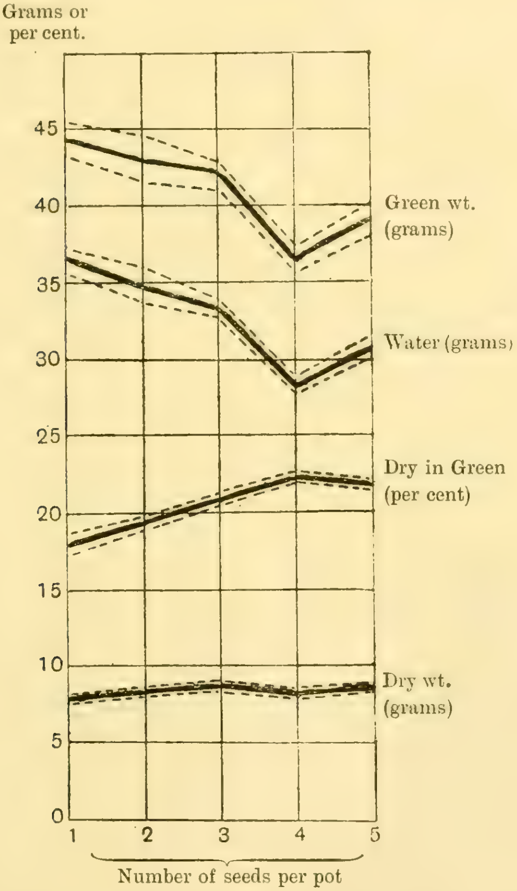


Fig. 1. Curves showing the amount of green weight, dry matter and water (in grams) and the percentage of dry matter in green weight when varying numbers of mustard plants were grown in 10 kilos of soil (tall pots).

The average results for the ten pots with each rate of seeding are set out in Table I and Fig. 1. The quantity of dry matter produced per pot is practically identical in each case, as the variations fall within the limits of experimental error. This indicates that the nutritive functions are severely limited by some factor of competition which cuts down the normal activities of the plants in proportion to the number of individuals that are struggling for existence in a similar bulk of soil. With 1, 2, or 3 plants per pot the amount of nitrogen taken up is identical, and it is evident that the whole of the nitrogen available for use as food was used by a single mustard plant under the conditions of experiment, and where more plants were grown per pot the individuals were unable to obtain as much as they could utilise. Probably therefore, the chief competitive factor in this case was the quantity of available nitrogen, as when once this was all absorbed the plants were unable to make further use of other nutritive substances. With 4 or 5 plants per pot, on the other hand, the whole of the available nitrogen was not taken up, the quantity lacking being slightly outside the limits of experimental error. At the same time a sharp drop occurred in the green weight, due entirely to the presence of less water, the dry weights being almost constant. In this case some other limiting factor, probably not nutritive, was apparently beginning to come into action, but the available data at this stage do not allow of any certainty as to its nature. With 4 or 5 seeds per pot the plants matured very much earlier, and by the time of cutting a considerable amount of desiccation had already occurred, which would account for the drop in water content but not for the reduced intake of nitrogen, both in actual weight and in proportion to the total dry matter.

The amount of water supplied to the pots was the same in every case, and the amount of dry matter formed per pot was constant, irrespective of the rate of seeding. Nevertheless the plants made very different use of the water, the thinly seeded plants retaining far more in their tissues, so that the succulence as shown by per cent. dry matter in green weight decreased steadily as the plants became more crowded, from 1 to 4 or 5 per pot, 4 and 5 per pot being alike in this respect. This is not merely a question of the quantity of water available for use by individual plants, as with constant supply and constant dry matter it would be theoretically possible to attain a similar degree of succulence in each case, but the interplay of the various factors of competition is such that the balance of the physiological processes is altered as crowding occurs and the response is partly in the direction of change of succulence.

On the whole, therefore, it is apparent that where a number of plants are growing in close association with a limited supply of food the quantity of available nitrogen sets a definite limit to the possible growth, and so is a very important factor in the competition between plants. Other factors are in play, however, and later experiments were designed to isolate the more important of these (see p. 151).

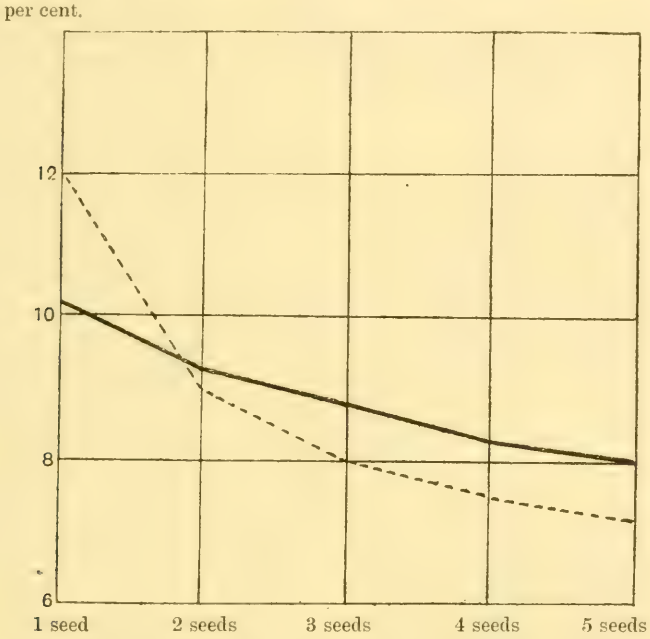


Fig. 2. Black line shows the efficiency index of dry weight production (per cent.) when varying numbers of mustard plants were grown in 10 kilos of soil (tall pots).

Dotted line shows the relative amount of food available per plant with each rate of seeding.

V. H. Blackman has recently put forward an important proposition indicating that the growth of an annual plant, at least in its early stages, follows approximately the "compound interest law[1]," the rate of interest or the percentage rate at which plant material accrues being termed the "efficiency index" of dry weight production. In the present experiment the reduction in the amount of dry matter produced by each individual plant with a decrease in the supply of available food is an expression of the alteration in the efficiency index, as the working capacity of the plant in this case is limited by the material with which it can build up its tissues.

---

[1] Blackman, V. H. (1919). "The compound interest law and plant growth." *Ann. Bot.* XXXIII, p. 357.

Table II. *Efficiency indices for* 10 *pots.*

Mustard.

	Range per cent.	Average efficiency index per cent.
1 seed per pot	10·5 —9·843	10·19
2 ,, ,,	9·475—8·895	9·247
3 ,, ,,	8·91 —8·558	8·734
4 ,, ,,	8·558—7·91	8·229
5 ,, ,,	8·161—7·796	7·969

Table II and Fig. 2 show graphically the steady fall in the efficiency index as the food supply gets less. The close correlation of cause and effect is shown by the dotted curve which represents the relative actual food supply per plant. Though the steepness of the curves varies, especially in the initial drop from 1 to 2 seeds, the direction changes in the same sense in every case, as the one factor follows in the wake of the other.

EXPERIMENT II.

Barley.

Narrow pots. 10 kilos soil.
  Seeds sown March 21st, 1917. One to five per pot after thinning.
  Plants cut July 16th, 1917.
Broad pots. 20 kilos soil.
  Seeds sown March 21st, 1917. One to eight per pot after thinning.
  Plants cut July 16th, 1917.

This test resembled Experiment I, but was carried out with a different plant, barley, to ascertain whether the response to competition was similar in two widely varying species. Two sizes of pots were used in this case in order to obtain further evidence of the correlation between the amount of growth and the quantity of available food.

From an early stage in the experiment the strength of the individual barley plants varied inversely as the rate of seeding, though the superiority of the thinly seeded plants was not so markedly evident as in the case of mustard. The same relative position was maintained to the time of harvesting, when the thinly seeded plants were better developed and much less mature than the more crowded specimens. In all cases the lower leaves were ripe and brown, but the ears varied considerably in maturity from greenish grains with green awns (1 plant per pot) through various stages of yellow coloration to dead ripe grains with dull brown awns (5 plants or 8 plants per pot). In the single plants the straw was thick, the leaves broad and well developed and the ears rather numerous, and these plants were also rather taller than any of the others. As the number of plants increased the stems became thinner, the leaves narrower and the ears fewer, and in all cases the more crowded the plants the more mature they were. This hastening of maturity is probably associated with the varying quantity of water available per plant, as it is well known that in a dry season when little water can be obtained cereals and other crops ripen off more rapidly in response to the drought.

Table III. *Average results per narrow pot* (*average of* 10 *pots*).

No. of plants	No. of ears	Green wt. gms.	Dry wt. gms.	% dry in green	Water present gms.	% N in dry	Actual N gm.
1	9·1	56·77 ± 2·72	25·86 ± 1·09	46·28 ± 1·04	30·91 ± 1·63	·776 ± ·016	·199 ± ·0068
2	10·4	58·09 ± 1·47	27·22 ± ·35	47·29 ± ·90	30·87 ± 1·12	·748 ± ·010	·203 ± ·004
3	11·5	55·10 ± 1·43	26·98 ± ·61	49·07 ± ·65	28·12 ± ·82	·766 ± ·009	·207 ± ·005
4	11·3	51·99 ± 1·69	26·05 ± ·50	50·91 ± 1·36	25·94 ± 1·19	·771 ± ·009	·201 ± ·003
5	12·8	57·76 ± 1·12	27·87 ± ·37	48·38 ± ·44	29·89 ± ·75	·734 ± ·010	·204 ± ·003

Table IV. *Average results per broad pot* (*average of* 3 *pots*).

No. of plants	No. of ears	Green wt. gms.	Dry wt. gms.	% dry in green	Water present gms.	% N in dry	Actual N gm.
1	14·3	125·97	51·64	40·88	74·33	·778	·3998
2	16·3̇	108·53	49·66	45·76	58·87	·783	·4162
3	19·3̇	115·03	52·33	45·59	62·70	·744	·3881
4	20·0	116·76	53·69	42·76	63·07	·771	·4141
5	19·0	106·89	52·15	49·05	54·74	·809	·4219
6	20·0	109·07	52·55	48·15	56·52	·759	·3982
7	23·0	109·46	53·29	48·86	56·17	·753	·4014
8	24·0	105·34	51·16	48·57	54·18	·792	·4050

In the narrow pots the numerical results were very similar whatever the rate of seeding, except that rather more ears were produced per pot with an increase in the number of plants. The actual amount of nitrogen extracted was practically identical in each case, again indicating that the amount of available nitrogen was one of the chief, if not the chief, factors in determining the amount of growth. The results obtained with the broad pots were much the same. The amounts of dry matter produced and the nitrogen extracted showed little variation from set to set, but were just twice as great as in the narrow pots, as twice the amount of soil and therefore twice the quantity of plant food was available. This affords yet more conclusive evidence that under the conditions of this experiment the amount of growth possible was strictly dependent on the available nitrogen, irrespective of the number of plants. A comparison of the figures for individual plants (Table V) shows that the amount of dry matter produced and nitrogen extracted is practically proportional to the amount of soil available and therefore to the quantity of plant food, especially nitrogen, and also that a given quantity of soil only admits of a given amount of growth.

It is interesting to notice that while barley was able to extract ·20 gm. N from each tall pot, mustard only took away ·14 gm. This may be due to the longer period over which the barley was grown, or possibly to some essential difference in the absorptive action of the two plants.

Table V.

Broad pots				*Narrow pots*			
No. of plants per pot	Green wt. per plant gms.	Dry wt. per plant gms.	Total N removed per plant gms.	No. of plants per pot	Green wt. per plant gms.	Dry wt. per plant gms.	Total N removed per plant gms.
* 2	54·26	24·83	·2081	1	56·77	25·86	·1990
4	29·19	13·42	·1035	2	29·05	13·61	·1017
6	18·18	8·76	·0664	3	18·37	9·00	·0688
8	13·17	6·39	·0506	4	13·00	6·51	·0502

* As the broad pots contained twice as much soil as the narrow ones, each plant in the broad pots with 2, 4, 6, 8 plants had the use of the same amount of soil as 1, 2, 3, 4 plants respectively in the narrow pots.

Table VI. *Efficiency Indices. Barley.*

For 10 *tall pots.*

	Range	Average efficiency index
1 seed per pot	5·419—4·966	5·258
2 ,, ,,	4·796—4·578	4·712
3 ,, ,,	4·431—4·023	4·358
4 ,, ,,	4·151—3·927	4·080
5 ,, ,,	4·021—3·858	3·948

For 3 *broad pots.*

	Range	Average efficiency index
1 seed per pot	5·933—5·708	5·852
2 ,, ,,	5·305—5·055	5·225
3 ,, ,,	4·952—4·876	4·922
4 ,, ,,	4·712—4·674	4·701
5 ,, ,,	4·536—4·431	4·483
6 ,, ,,	4·382—4·254	4·334
7 ,, ,,	4·256—4·190	4·214
8 ,, ,,	4·163—4·130	4·147

The association between the amount of growth and the quantity of soil available is further demonstrated by the efficiency indices of the barley with different rates of seeding (Table VI), the index decreasing steadily with the increase in the number of seeds per pot. Fig. 3 shows this even more strikingly. As the large pots contain exactly twice as much soil as the narrow pots, two seeds in large pots each have as much soil and therefore food available as one seed in the narrow pots, four in large as two in narrow, etc. Consequently in the figure the efficiency indices for both sets of pots are plotted together according to the quantity of soil available for individual plants, and the curves are practically coincident, showing again how entirely dependent the growth is on the available food supply.

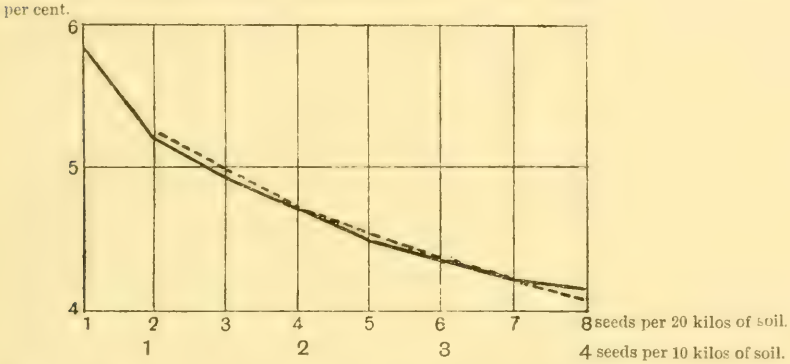


Fig. 3. Black line shows the average efficiency indices for varying numbers of plants grown in 20 kilos of soil (broad pots).
Dotted line ditto in 10 kilos of soil (tall pots).

2. EFFECT OF INDIVIDUAL FACTORS ON COMPETITION.

The above experiments with mustard and barley show that if the food supply in the soil is restricted this will be the chief limiting factor in determining the amount of possible growth, and therefore the action of other factors of competition will be less obvious. On the other hand, these other factors are at work at the same time under these conditions so that the results obtained are not necessarily solely due to competition for food. In order, therefore, to ascertain the working of the various factors it is necessary to arrange experiments in which each may be studied individually, without interference by the others.

A. INFLUENCE OF FOOD SUPPLY ON COMPETITION.

Proof of the close relation between the quantity of available food and the amount of growth made was obtained from several sets of water cultures carried out with barley and wheat in 1915. The plants were grown in four food solutions of different strengths, the usual culture solution[1] (called N for convenience) and others one-fifth, one-tenth, and one-twentieth as strong $\left(N, \frac{N}{5}, \frac{N}{10}, \frac{N}{20}\right)$. Each experiment (three in all) was carried on for six weeks, three series being run at the same time. In one the nutrient solution was changed every four days, in the second it was changed once (half-way through the test), and in the third no change was made at all. The plants were spaced at equal distances apart, so that each received a similar light supply. In every case it was found that the dry weights of the plants decreased coincidently with the strength of the nutrient solution. Even where the solutions were constantly changed the $\frac{N}{20}$ or $\frac{N}{10}$ plants were very much behind the N plants, showing that the total quantity of available food had a direct bearing on the amount of growth. When the solutions were changed but once, or not at all, the $\frac{N}{5}$ plants were considerably weaker than the N, as they had apparently not received as much food as they could deal with. When the solutions were frequently changed, however, the $\frac{N}{5}$ plants did not fall nearly so much behind the N, indicating that the total amount of food supplied in the solution with constant changing enabled the plants to make almost their maximum growth, while the N plants probably received more food than they could profitably deal with[2]. (Fig. 4.)

Thus, when the competition of one plant with another for food is removed, and when the water supply is adequate and all plants receive a similar and plentiful supply of light, it is seen that up to a certain limit the amount of growth is proportional to the supply of food, though

[1]

Potassium nitrate	1 gm.
Magnesium sulphate	·5 ,,
Calcium sulphate	·5 ,,
Potassium di-hydrogen phosphate	·5 ,,
Sodium chloride	·5 ,,
Ferric chloride	·04 ,,

Distilled water—to make up 1 litre.

[2] Brenchley, W. E. (1916). "The effect of the concentration of the nutrient solution on the growth of barley and wheat in water cultures." *Ann. Bot.* XXX, 77–90.

above that limit the plants are unable to make full use of their supply. This, then, may be regarded as an argument for giving crops a fair amount of room in order that they may obtain sufficient food, though too thin planting may be wasteful as the plants may be unable to make the best use of the available food.

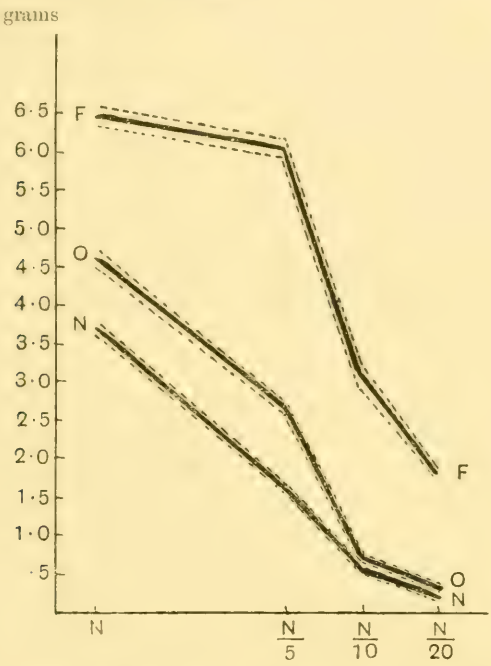


Fig. 4. Average dry weights of ten barley plants grown in water cultures in nutrient solutions of different concentrations. Dotted lines show limits of probable error.

F. Solutions changed every four days.
O. Solutions changed once during experiment.
N. Solutions never changed.

B. LIGHT AS A FACTOR IN COMPETITION.

Although it is always stated that overcrowding of plants leads to great competition for food and light, still little or nothing is definitely known as to the extent to which competition for light affects the growth of plants. As overcrowding increases, both factors come more and more into play, and under ordinary cultural and experimental conditions it is impossible to separate the two and to attribute any proportional action to one or the other. The first experiments described above (pp. 144–151) showed clearly how powerful a factor a limited food supply is, but no evidence was obtained as to the action of the light factor. To elucidate this point water cultures were set up in which no shortage of food or water was allowed to occur, but in which the light supply was varied by the conditions of spacing. Sixty-four barley plants were placed separately in nutrient solution and the bottles were packed in a square with eight plants per side, as closely as possible, the distance from plant to plant being 3½ inches. Another 64 bottles, each with its plant, were arranged on the greenhouse benches in the immediate vicinity of the crowded set, but in this case each bottle was at least one foot away from its nearest neighbour. Each bottle was kept in the same place throughout the experiment, the nutrient solution being constantly changed to prevent any lack of food or water introducing another factor of competition. In this way it was hoped to obtain conditions of dense overcrowding on the one hand, and absolute freedom from light competition on the other, and the result justified the means.

For the first five or six weeks, while the barley plants were quite small and no overlapping of leaves occurred no difference was observed in the growth of the spaced and crowded plants. As tillering began, the crowded plants gradually seemed to improve more rapidly than the spaced ones, though for some time it was doubtful if this were not merely an optical illusion. After eight weeks' growth it was obvious that the crowded plants were really the better. The leaves were decidedly larger and broader, of a much darker green, while the spaced plants were narrower in leaf and of a lighter yellowish colour, some plants showing a tendency to chlorotic stripes. At this stage a wet and dry bulb thermometer was inserted amongst the leaves of the crowded plants, and another was placed in the greenhouse away from the foliage. The difference rapidly became still more marked, and a week later photographs were taken (Plate V, figs. 1 and 2).

For the sake of a fair comparison the spaced plants were temporarily crowded together (Plate V, fig. 2) in order to avoid giving the crowded plants an unfair advantage due to optical illusion.

A little later the succulence of the crowded plants was very noticeable, the texture recalling that of marsh plants. The stems were very fleshy and the plants, especially in the middle of the square, had begun to depend upon their neighbours for support. The spaced plants at this time appeared to be rather more tillered, and the tillers took full advantage of the available space and spread out in rosettes on the tops of the bottles. The leaves and shoots were much tougher and less easily broken than those of the crowded set. About this time or a little earlier differences began to manifest themselves between the plants in the various parts of the crowded square. Those in the outside rank were well tillered, with plenty of good strong healthy leaves, but as the middle of the square was approached the number of tillers began to grow less and the plants became lanky, thin, and much less healthy. At this stage the assistant who constantly handled the plants in changing the solution expressed the opinion that the spaced plants would probably prove better in the long run than the crowded plants, in spite of the broad hefty leaves of the latter, an opinion that later events proved to be justified.

All the plants began to show ears at about the same time, in spite of the various differences in maturity of the two sets. The spaced plants were looking very unhappy, as the lower leaves changed colour and died down badly, while the tillers were not nearly as tall as in the crowded set. The crowded plants, on the other hand, retained their dark green colour, and although maturity was much less advanced as regards vegetative growth the ears were fully as advanced as in the spaced set. The ocular difference between the two sets reached its zenith at this time, the contrast between the narrow yellowish withering leaves of the spaced plants and the broad dark-green succulent leaves of the crowded ones being most striking. A few days of excessive heat supervened at the end of the experiment and all the plants showed the effect. Almost all the leaves of the spaced set ripened off, and were yellow and withered, but the plants were well tillered, with stout dry stems and well-developed ears. Little mildew was present though a good deal of aphis was about. The leaves of the crowded plants had also begun to die off, but became flaccid and reddish instead of being rather stiff and yellow. The ear and grain formation of the outer plants of the square were ahead of the spaced set, but the middle plants showed little fructification and were becoming slimy at the base of the stems, which were sappy and easily bent. Mildew was much more prevalent but less aphis occurred than on the spaced plants.

At this stage each plant was taken off, the roots were carefully washed in two changes of clear water to remove adherent food salts, and the dry weights were ascertained after several days drying in the drying room at a temperature of 80°–90° F. The number of ears and the number of stalks per plant were counted before cutting up.

The comparison of the spaced and crowded plants at various stages of growth and after drying yields several interesting and rather surprising results. According to the usual conception of things dense overcrowding produces thin, unhealthy plants, badly drawn up, with few and small leaves often of a bad colour, whereas plants with plenty of space become stout and stocky, with a large area of healthy leaves. In the present instance overcrowding was apparently favourable to growth for some long period, as the plants became so much larger, with very broad leaves of an intensely dark colour, while the corresponding spaced plants were considerably smaller, with narrow pale leaves, which tended to die off at a rather early stage. The reason for this reversal of the usual order of things is not obvious, but certain suggestions may ultimately throw some light upon it. The experiments were carried on in a roof greenhouse which receives plenty of sun and tends to become very hot at times. The range of temperature during the course of the experiment is shown in Table VII.

Table VII.

1919	Maximum	Minimum
March 1—31	44°— 72° F.	26°—52° F.
April 1—30	64°— 95°	32°—52°
May 1—31	64°—110°	32°—56°
June 1—20	68°— 99°	40°—59°

Strong sunlight tends to check growth to some extent, and as the spaced plants were each so far separated from their neighbours as to permit of no shading, the insolation had full play and possibly kept back leaf development. The strong light may also have had some effect upon the chlorophyll, preventing it from attaining a very deep colour. The crowded plants cast considerable shade on one another thereby reducing the insolation, and this may have enabled the plants to form longer and broader leaves as growth was less checked by the light, while the chlorophyll developed a very full deep colour. The amount of shading, however, did not seem to be sufficient to account for the marked difference in external appearance, and other factors were sought for. The wet and dry bulb thermometers which were kept in the house and among the crowded leaves showed that except on rare occasions the humidity of the air among the crowded plants was greater than that in the free air of the house. The range of variation was very considerable, reaching to as much as 50 per cent. saturation, as is shown in Table VIII.

The character of the crowded leaves suggests a correlation with this difference of humidity. The succulence and slight fleshiness of these leaves recalls those of plants growing in very moist places, in marshes or by water, where the air is naturally always moist even in hot weather, while the dry harsher leaves of the spaced plants may well be correlated with the relatively low humidity of the air with which they are surrounded. The marked difference in humidity might not occur out of doors where there is a freer circulation of air than in a greenhouse, and the absence of this extra moisture when plants are crowded in the field may account for the fact that the excessive leaf growth in barley under these conditions is not a usual occurrence. The extra growth of the crowded plants at this stage is not caused by a higher temperature among the leaves, as almost every day the dry bulb in this position registered a *lower* temperature than that exposed to the free air of the greenhouse.

Table VIII.

Difference between humidity of house and humidity among plants. Percentage of saturation	Number of days difference was recorded
Humidity among plants *higher* than humidity of house.	
0—10	8
11—20	8
21—30	10
31—40	5
41—50	1
Total	32
Humidity among plants *lower* than humidity of house.	
0—10	4
11—20	2
21—30	1
31—40	1
Total	8

For several weeks it appeared as though, contrary to all accepted notions, the crowded plants were going to produce better plants and a larger crop than those that had had plenty of room. As has been already recorded, however, signs of deterioration gradually set in, especially among the plants in the middle of the square, and by the time the plants were cut marked differences were noticeable. The chief points of difference are noted under their several heads.

1. *Number of ears.* When the ears were counted half the crowded plants possessed none at all, while all the spaced plants but three had one or more, thirty-nine of them possessing from 6–8 ears apiece. *In toto* the 64 crowded plants only produced 178 ears while the 64 spaced ones had 362, more than double the number being formed when adequate

room for growth was available. The number of plants with various numbers of ears was as follows:

Number of plants with specified numbers of ears.

No. of ears per plant	Crowded plants	Spaced plants
0	32	3
1	3	3
2	2	3
3	4	6
4	3	5
5	3	1
6	4	13
7	4	14
8	4	12
9	3	3
10	1	—
11	1	1

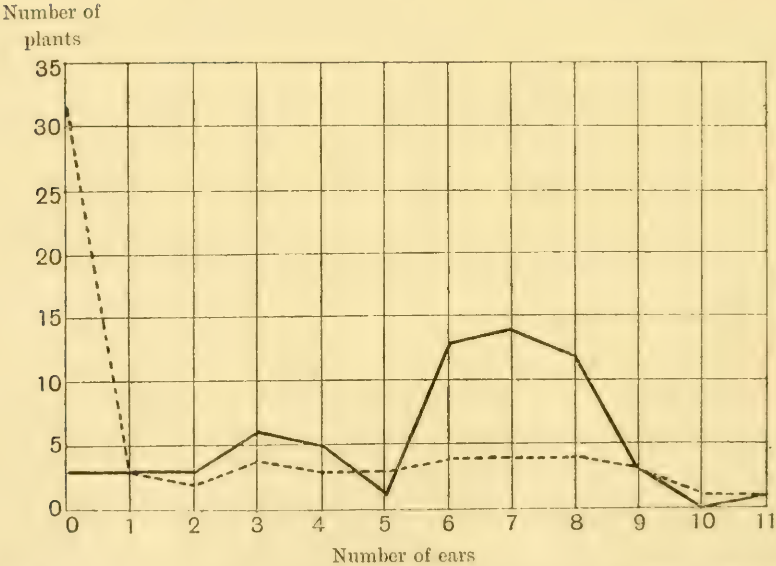


Fig. 5. Curves showing the number of barley plants with various numbers of ears when grown under conditions of (1) crowding, (2) adequate spacing. 64 plants in each set.
Black line—spaced plants.
Dotted line—crowded plants.

The above figures are graphically expressed in Fig. 5. As such a large proportion of the plants have from 6–8 ears this may be regarded as a standard type.

The spaced plants occupied a rather large area of bench in the greenhouse surrounding the crowded square. The greater number of the plants which only formed a few ears (from 0–3) were grouped together at one end of the house which is occasionally slightly shaded by other parts of the structure. This concentration may be merely coincidence, or it may be due in some way to less advantageous conditions than the rest of the plants endured. The rest of the bench space was more equally illuminated, and the plants with similar numbers of ears were well distributed and not grouped at all. In the crowded set the number of ears per plant depended very largely upon the position in the square. The majority (22 out of 28) of those in the outer rank produced ears varying in number from 1–11 whereas only 10 plants in 36 in the inner squares had any ears at all, from 1–9. The distribution is shown in the diagram (Fig. 6), which gives the number of ears for each plant occupying a certain position in the square.

2	0	7	8	0	0	1	0
7	0	0	0	0	0	7	5
4	0	6	0	0	3	4	6
4	3	0	0	0	0	0	0
0	0	0	0	1	0	1	3
3	0	0	0	0	0	2	10
9	6	0	0	0	0	9	7
11	8	8	5	6	5	8	9

Fig. 6. Diagram showing the number of ears produced by each of 64 crowded barley plants in the positions they occupied during growth.

The crowding, therefore, was very disadvantageous to the production of ears, and the paucity of fruiting stems in the inner parts of the square supports the idea that overcrowding in the field may have a very definite tendency to reduce the crop by weakening the plants below fruit bearing standard.

2. *Number of tillers per plant.* Apart from the ears produced the number of tillers thrown out by each plant is instructive. 62 out of 64 spaced plants had from 8–20 tillers and of these more than half possessed from 10–12 stalks, no plants showing less than 8. Overcrowding, however, tended both to decrease and increase the number of stalks, widening the range of variability in this respect. This suggests that when no competition for light occurred the plants tended towards the production of a standard number of stalks, whereas when competition was very keen each plant, in playing for its own hand, produced a number of stalks in accordance with the particular advantage or disadvantage it gained. (Fig. 7.)

With the spaced plants the position in the greenhouse had no bearing on the tillering, but in the crowded square the outside rank carried the largest number of stalks per plant, the second rank came a bad second, while the two innermost squares bore the smallest numbers of tillers, which were of a weakly character. In this respect the amount of tillering and ear formation ran parallel. (Fig. 8.)

Where the plants had sufficient space some correlation occurred between the number of tillers produced and the number of ears formed, but when they were crowded this correlation disappeared. In the spaced plants nearly all the plants with ears had 8–18 stalks, while the largest number of the standard 6–8 ears (see p. 158) were produced on plants with 10–14 stalks, very few being outside this limit, thus roughly speaking every other tiller bore an ear. Among the crowded plants most of those with 4–12 tillers bore no ears at all, the ears being usually produced by plants with 14–26 stalks, but no regular increase in the number of ears occurred with increased tillering. Adequate spacing, therefore, tends to reduce the number of tillers per plant that are necessary to produce a certain number of ears, and also causes a tendency towards a certain standard plant in which the number of tillers and ears formed vary within rather narrow limits. With overcrowding this standard plant disappears, and the amount of tillering gives no index of the number of associated ears.

3. *Comparative dry weights of plants.* The dry weights of the barley plants bore out the observations that adequate spacing tends to the production of a more even type of plant, while crowding accentuates

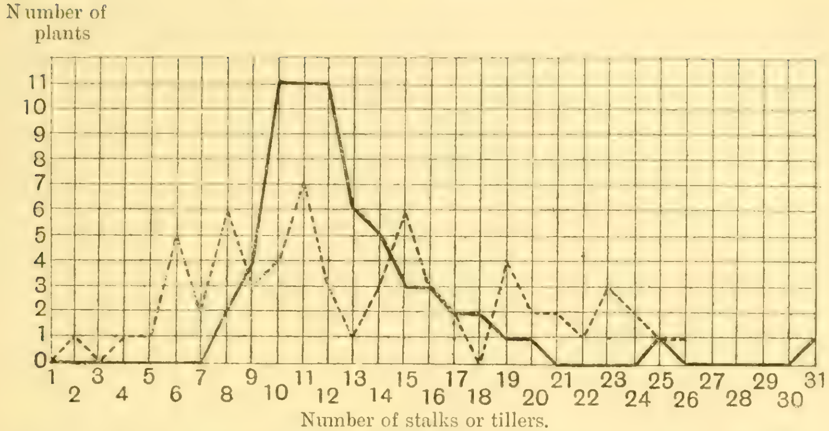


Fig. 7. Curves showing the number of barley plants with various numbers of tillers when grown under conditions of (1) crowding, (2) adequate spacing. 64 plants in each set. Black line—spaced plants. Dotted line—crowded plants.

25	11	19	14	24	21	15	23
23	7	11	6	8	11	14	20
16	11	8	8	8	9	15	17
24	19	7	8	6	10	9	21
26	10	11	2	11	6	6	23
19	11	5	6	4	12	10	15
15	17	14	12	9	8	13	15
12	10	16	19	20	22	15	16

Fig. 8. Diagram showing the number of tillers produced by each of 64 crowded barley plants in the positions they occupied during growth.

the difference between individuals and also prevents all the growth possible being made. The extreme range of weight is large even under favourable circumstances, but is greatly increased when the competition for light comes into play. The figures in Table IX show that this is the case with both the root and shoot, the extension of range in both cases being chiefly downwards owing to the hindrance to growth caused by crowding.

Table IX. *Total range of dry weights.*

	64 crowded plants gms.	64 spaced plants gms.
Shoot	·50—24·44	9·72—24·47
Root	·37— 5·57	1·52— 6·27
Whole plant	·97—30·01	12·34—28·74

The result of this downward range is to decrease the total amount of dry matter produced by a given number of crowded plants, and so to lower the average weight, as is shown in Table X.

Table X. *Total and average dry weights.*

	64 crowded plants		64 spaced plants	
	Total gms.	Average per plant gms.	Total gms.	Average per plant gms.
Shoot	778·89	12·17	1174·43	18·35
Root	123·32	1·92	256·58	4·01
Whole plant	902·21	14·09	1430·91	22·36

The total range and average weights, however, hardly give a fair picture of the general effect of overcrowding on the majority of the plants, and with such a large variation in weight the average is in reality of little value. A much clearer idea is obtained by a comparison of the interquartile range of the weights under the different conditions, as by this means the most abnormal plants, both large and small, are ruled out and only the more representative specimens come under consideration (Table XI).

Table XI. *Interquartile range (of 32 intermediate plants in each case).*

	64 crowded plants			64 spaced plants		
	Actual range gms.	Diff. gms.	Diff. / Lowest wt. of range	Actual range gms.	Diff. gms.	Diff. / Lowest wt. of range
Shoot	6·07—18·59	12·52	2·06	16·54—20·54	4·0	·24
Root	·95— 2·82	1·87	1·97	3·47— 4·52	·85	·25
Whole plant	7·22—21·84	14·62	2·03	20·46—25·04	4·58	·22

These figures are far more instructive than those previously dealt with. They lay strong emphasis on the fact that overcrowding hinders even development whereas if sufficient room is available the plants tend in both root and shoot towards the production of a fairly uniform amount of dry matter—i.e. towards a more or less uniform growth. With overcrowding the difference between the greatest and least weight of the range is just twice the least weight, with shoot, root, and whole plant, whereas in the spaced plants the difference is so small that it only amounts to ¼ the least weight of the range, one-eighth of that with the crowded set. This corroborates and justifies the statement made earlier in this paper that, other things being equal, in the absence of competition for light there is a tendency towards the production of a standard type of plant.

19·12	11·07	24·41	23·31	19·27	12·94	14·34	20·12
21·84	11·10	8·69	3·29	5·94	6·29	15·20	22·21
23·02	7·94	13·94	5·84	5·90	10·16	14·81	19·71
23·06	14·66	4·79	6·19	5·39	7·44	8·77	15·04
18·29	6·32	9·51	0·97	9·89	6·07	5·82	21·44
13·74	7·04	2·64	3·74	2·92	10·59	11·17	23·67
26·11	23·11	9·47	10·34	8·49	7·22	23·76	22·97
30·01	19·70	26·87	23·91	19·27	21·96	23·51	25·86

Fig. 9. Diagram showing the number of grams of dry matter produced by each of 64 crowded barley plants in the positions they occupied during growth.

The actual effect of light competition on individual plants is clearly shown by the dry weight at different points of the crowded square. (Fig. 9.)

The plants in the outer rank are less subject to light competition than any of the others, as they are quite free and exposed on one side; most of these are fairly heavy, 14 out of 28 plants (50 per cent.) being above the upper limit of weight of the interquartile range, and none below it. The second rank suffers from the proximity of its healthy neighbours of the outer row, and is also flanked by others on the inner side, with the result that only 10 per cent. (2 out of 20) are above the upper limit and 35 per cent. (7 out of 20) are below the lower limit of the interquartile range. The third rank is worse still, with no heavy plants, but with 58 per cent. (7 out of 12) below the lower limit of range, while the innermost core of the square consists of four plants suffering most severely from the light shortage, 3 of them (75 per cent.) being below the lowest limit and the fourth not far above it. These results show more clearly when tabulated (Table XII).

Table XII.

		Above upper limit of interquartile range		Below lower limit of interquartile range	
	Number of plants	Number of plants	Percentage	Number of plants	Percentage
Outer rank	28	14	50	0	0
Second rank	20	2	10	7	35
Third rank	12	0	0	7	58
Fourth rank (inner core)	4	0	0	3	75

The depreciation in growth caused when even so small a number of plants as 64 are crowded is thus very great, and it is obvious that if the number were increased the total depreciation would be greatly augmented, as all the plants within the outer row or two of the mass would feel the effect of competition most severely. It is not a question of competition for food by the roots as every plant had its own individual supply which was never allowed to run short, but the competition for light prevented the inner plants from making adequate use of their mineral resources, and less dry matter was produced in consequence.

The physiological effect of this struggle for light finds morphological expression in the relations between the roots and shoots of the competing plants. In every case a full quantity of nutrients was supplied to the roots, but the amount of light available to carry on elaboration of sap and assimilation of carbon-dioxide in the leaves varied with the individual plant. When overcrowding occurred this implied a lessened supply of prepared nutrient material for building up the tissues and it appears as if the plants attempted to dispose of this restricted quantity in order to combat the disadvantage as much as possible. With increased crowding the tendency is for the weight of the root to decrease more rapidly than that of the shoot, so that the shoot/root ratio goes up. In other words, the plant tends to utilise a larger proportion of its elaborated food in laying down new leaf tissue, possibly in an attempt to increase its assimilatory surface in order to make the most of the diminished supply of light at its disposal. The corresponding reduction in root tissue is economic as it is useless for more dissolved mineral food to be absorbed than can be dealt with by the leaves. The range of variation in the shoot/root ratio is greater with the crowded than with the spaced plants, corresponding again to the greater deviation of the competing plants from the standard type.

Table XIII. *Shoot/Root ratio.*

	Crowded plants	Spaced plants
Total range	1·064—13·57	3·005—8·482
Interquartile range	5·235— 7·906	3·98 —5·358

		Below lower limit of interquartile range		Above upper limit of interquartile range	
	Number of plants	Number of plants	Percentage	Number of plants	Percentage
Outer rank	28	11	39·3	5	17·8
Second rank	20	3	15·0	3	15·0
Third rank	12	1	8·3	5	41·6
Fourth rank (inner core)	4	1*	25*	3	75·0

* This plant was so abnormally weak in the shoot that it is not fair to include it in the consideration of the figures as the low shoot/root ratio in this case is simply due to the failure of the shoot to develop.

These figures of Table XIII lend numerical support to the idea that with increasing competition for light the growth of the shoot is made more and more at the expense of the root, so that the shoot/root ratio gets steadily larger. With an abundant supply of room, on the other hand, a more stable equilibrium is reached, a larger development of root in proportion to shoot occurs, and consequently the shoot/root ratio is lower, particularly when the interquartile range is considered.

4. *Efficiency Index of dry weight production.* The efficiency index or rate of addition of dry matter of the individual plant shows more clearly than anything else how much the growth economy is affected by variation in the available light.

Table XIV. *Efficiency Index of spaced plants.*

	Range	Difference in range	
Total range	4·265—4·955	·690	
Interquartile range	4·678—4·842	·164	
First (lowest) quartile	4·265—4·662	·397	
Second quartile	4·678—4·777	·099	·264
Third quartile	4·790—4·842	·052	
Fourth (upper) quartile	4·842—4·955	·113	

The efficiency indices of the spaced plants cover a comparatively small range (Table XIV), while the interquartile range is very small. The lowest quartile includes all those plants which from one cause or another are weaker than their fellows, and the variation in efficiency of these plants is greater than that of all the rest. This indicates an approach to a certain standard of efficiency in the majority of the plants—i.e. that under the prevailing conditions in the greenhouse a certain quantity of growth is possible in the given time, and a large proportion of the spaced plants approximate to this standard. The increased deviation on the part of the minority may be due to the somewhat excessive insolation referred to earlier in this paper, which would tend to depress the growth of any plants that were naturally at all weakly. The variation in the rate of growth of the spaced plants may therefore be attributed to the different response of the individuals to their environment when they are not influenced by the proximity of other vegetation and are therefore free from competition.

The efficiency indices of the crowded plants reveal a very different state of affairs. The total range is very large, 2·199–4·989 per cent. per day[1]—and the interquartile range runs from 3·831–4·729, a far wider deviation than in the spaced plants. The average efficiency of the crowded plants as thus shown is lower than that of the others, and the approximation to the standard growth is considerably less.

Table XV. *Efficiency Index of crowded plants.*

	Range	Difference in range
Total range	*3·012—4·989	1·977
Interquartile range	3·831—4·729	·898
First (lowest) quartile	*3·012—3·811	·799
Second quartile	3·831—4·304	·473
Third quartile	4·353—4·729	·376
Fourth (upper) quartile	4·734—4·989	·255

* The index of the very weakly plant (2·199) is omitted.

---

[1] 2·199 is the index for the one exceptionally weak plant in the series, but even if this is rejected the range runs 3·012–4·989 per cent. per day

An interesting feature is the very gradual closing up of the range of variation from the lowest (first) to the highest (fourth) quartile, when compared with the sudden change from the first to the second among the spaced plants.

4·623	4·178	4·809	4·784	4·630	4·304	4·388	4·664
4·729	4·179	3·980	3·190	3·672	3·719	4·436	4·744
4·772	3·908	4·365	3·658	3·665	4·118	4·416	4·649
4·774	4·406	3·496	3·705	3·593	3·855	3·990	4·126
4·585	3·723	4·057	2·199	4·086	3·689	3·654	4·718
4·353	3·811	3·012	3·295	3·095	4·142	4·185	4·795
4·877	4·777	4·050	4·123	3·962	3·831	4·799	4·771
4·989	4·649	4·898	4·807	4·629	4·734	4·790	1·869

Fig. 10. Diagram showing the efficiency index of dry weight production for each of 64 crowded barley plants in the positions they occupied during growth.

Table XVI.

	Total no. of plants	Lowest quartile 1st		2nd quartile		3rd quartile		Upper quartile 4th	
		No. of plants	%	No. of plants	%	No. of plants	%	No. of plants	%
Outer rank	28	0	0	2	7	12	43	14	50
Second rank	20	6	30	9	45	3	15	2	10
Third rank	12	7	58·3	4	33·$\dot{3}$	1	8·3	—	0
Inner rank	4	3	75	1	25	—	0	—	0

Table XVI and Fig. 10 show that in the outer rank, where least competition occurs, 50 per cent. of the efficiency indices are in the highest and nearly all the rest in the third quartile. In the second rank where the competition is already rather great, the efficiencies vary considerably, being spread over the whole range with a heavy concentration in the two lowest quartiles. In the two innermost ranks, however, the efficiencies are very low, the larger percentage in each case being in the lowest quartile and none in the uppermost. These results prove graphically that, other things being equal, the degree of competition for light brought about by close spacing or crowding has a direct bearing on the efficiency of the plant in the production of new material. The greater the competition, the lower the efficiency, and consequently the lower the ultimate crop. Furthermore the balance of the plant economy is disturbed, and greater deviations from the standard type are induced, owing to the tendency to individual variation under similar conditions being encouraged and accentuated by the action of a competitive factor, which in this case is light.

5. *Nitrogen Content.* The total amount of nitrogen present in the spaced as compared with the crowded plants was 21·22 gms. against 18·22 gms., the larger total intake corresponding with the larger crop. The percentage of nitrogen, however, was lower in the spaced plants, being only 1·827 against 2·339. This implies that when the plants had sufficient space they were able to produce a larger amount of dry matter with a lower utilisation of nitrogen, and that although an abundance of nitrogen was supplied they did not make such inroads on it as would correspond with the excess of dry matter ultimately produced.

The difference in the degree of maturity of the two sets is reflected in the relative percentage of N in the straw and ears. Earlier work at Rothamsted[1] has shown that the percentage of nitrogen in the straw falls steadily from the time the grain begins to form, and that in the grain, after a slight initial fall, it rises steadily till maturity is reached. The spaced plants were much the more mature, and whereas the ears contained 3·432 per cent. N, the straw was so depleted that only 1·654 per cent. was present at the time of cutting. The crowded plants were still green and sappy, and the immigration from straw to ear was far less advanced, so that 2·273 per cent. N was still present in the straw, and the ears only possessed 2·959 per cent. Separate estimations were made for the different ranks of the crowded square, but no definite gradation in nitrogen content was observed throughout. In the outer rank, though, in which ear formation was further advanced than in the interior of the square the percentage of nitrogen in the grain was higher than the average (3·02 per cent.) and in the straw was lower (2·08 per cent.) thus following the normal law.

---

[1] Brenchley, W. E. (1912). "The Development of the Grain of Barley." *Ann. Bot.* XXVI, pp. 906, 917.

The above experiment with spaced and crowded plants proves conclusively how potent a factor is light competition in determining the growth of plants. Under ordinary conditions of cultivation overcrowding inevitably reduces the food supply of the individual plants, and, as was shown in the early part of this paper, this itself sets a limit to the amount of possible growth. This is widely recognised, but the effect of deficient light supply is less self-evident and therefore less taken into account. When plants are crowded in the field the root range is less circumscribed than when they are grown in pots and the available food supply is less restricted. The harmful effect of overcrowding under such circumstances is therefore probably due less to deficient nutrition than to light starvation which can occur, as shown above, even when a full and abundant food supply is assured. Further work on this point is needed, especially with regard to broad leaved plants in which the degree of overshadowing of one plant by another is accentuated, and in which possibly the factor of light competition is therefore even more important than with such narrow-leaved plants as barley.

SUMMARY.

1. The mutual action of one plant on another when grown in juxtaposition, usually known as competition, is a very complex phenomenon. Among the factors which come into play are competition for food, water and light, and also the possible harmful effect due to toxic excretions from the roots.

2. When the food supply is limited the dominant factor of competition is that of food and in particular the amount of available nitrogen. Other things being equal the total growth as measured by the dry matter produced is determined by the nitrogen supply, irrespective of the number of plants drawing on the resources.

3. With limited food supply the efficiency index of dry weight production decreases with the number of plants, as the working capacity of the plant is limited by the quantity of material available for building up the tissues.

4. The decrease in light caused by overcrowding is a most potent factor in competition even when an abundance of food and water is presented to each individual plant. With barley the effect of light competition is

(*a*) To reduce the number of ears.

(*b*) To cause great irregularity in the number of tillers produced.

(*c*) To reduce the amount of dry matter formed.

(*d*) To encourage shoot growth at the expense of root growth, thus raising the ratio of shoot to root.

(*e*) To increase the variation in the efficiency indices of dry weight production of a number of crowded plants, lowering them on the average.

(*f*) To decrease the power of the plants to make use of the food supplied to the roots, as evidenced by the total quantity of nitrogen taken up by similar numbers of plants when spaced out and crowded.

5. With adequate illumination (in barley) there is a tendency towards the production of a standard type of plant in which the relation between the number of tillers and ears, dry weights, efficiency indices, and ratios of root to shoot approximates within variable degrees to a constant standard. With overcrowding this approximation entirely disappears.

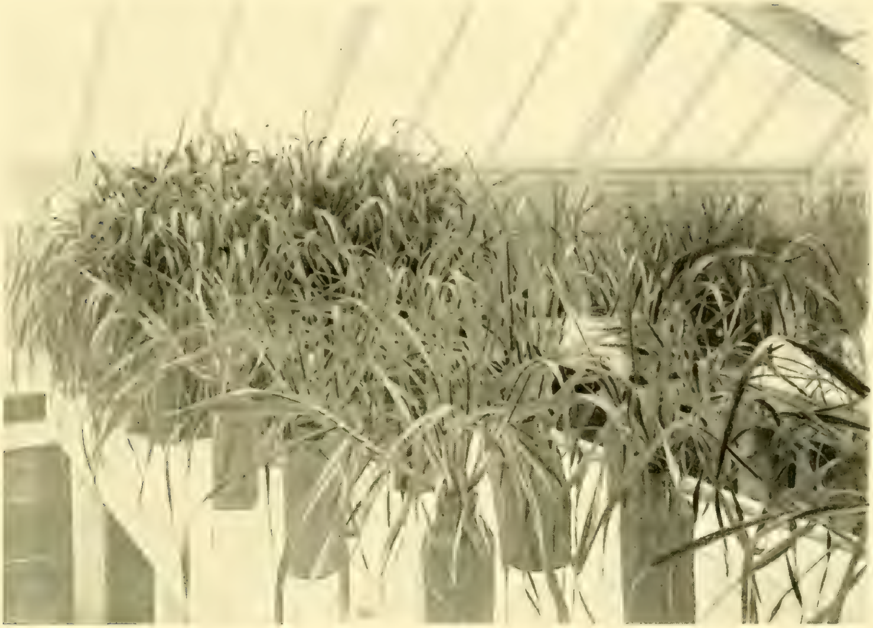


Fig. 1. Photo. of spaced and crowded barley plants as they stood during experiment. Crowded set at back on left, spaced plants in foreground.

Fig. 2. Photo. showing spaced barley plants temporarily placed close together for comparison with those that were permanently crowded during experiment. Crowded set on left, spaced set on right.

A CONTRIBUTION TO THE LIFE-HISTORY OF THE LARCH CHERMES (*CNAPHALODES STROBILOBIUS*, KALT.)[1].

By EDWARD R. SPEYER, F.E.S., M.A. (Oxon.),
Carnegie Scholar.

Formerly Lecturer in Economic Entomology at Oxford University and Tutor in Zoology to University College and Non-collegiate students. Recently special Entomologist and Acting Entomologist to the Government of Ceylon.

(With Diagram and Plates VI and VII.)

INTRODUCTION.

The insect commonly known as Larch Blight from the conspicuous white "wax-wool" which it secretes on the leaves of this tree during the spring and summer months, possibly has the most complex life-cycle of any member of the family Chermesidae. The Genus Chermes was established as such under the family Phylloxeridae, and in course of time, with the increasing discovery of species, became included in a Sub-family Chermesinae, containing several Genera, and finally in a family, embracing the Sub-families Phylloxerinae and Chermesinae.

There may be justification for this, but it is suggested that such a classification is a little premature, considering that the Sub-family Chermesinae comprises as many as seven genera, containing altogether only about twenty species.

Further, as an example, the Genera Chermes and Cnaphalodes have been differentiated through petty structural and morphological characters, which pale in the face of the greater and more prominent differences in habit and structure of the various generations of a single species.

Finally, these genera have been founded without any reference to the sexual individuals, descriptions of which, indeed, seem to be entirely lacking in the voluminous literature[1] on the structure and classification, and in the majority of cases without anything like a complete knowledge of the life-histories.

---

[1] The greater portion of this Paper is the result of an investigation made for the Delegacy of Forestry at Oxford University in 1913 and 1914. A report, embracing the material in detail, was submitted to the Delegacy in June, 1914, but does not appear to have been published.

The establishment of a new Genus for nearly every new species which comes to hand can surely be but a hindrance rather than a help to a sound systematic classification in the future.

Two species of Chermes in Great Britain are known to inhabit Spruce and Larch, respectively, as their host and intermediate host. Both form galls on Spruce and migrate to Larch by means of a winged parthenogenetic generation, and again return to Spruce by a similar winged generation, which, however, is different in details of structure and habit from the former.

Both these insects have received much attention recently, and an outstanding paper by Mr H. M. Steven, entitled "Contributions to the knowledge of the family Chermesidae," has been published in the *Proceedings of the Royal Society of Edinburgh*, vol. XXXVII, Part III, No. 21, June, 1917.

This paper supplies much information upon the life-cycles of the two Chermes mentioned, namely *Chermes viridis*, Ratz., and *Cnaphalodes strobilobius*, Kalt., and also upon the species of Cholodkovsky, which are confined to the Spruce only. It may be stated here that no discussion is advisable as yet upon the probability of the latter two species being identical with, and forming a phase of the life-history of, the two first-named species.

With regard to the nomenclature of the generations in the Chermesidae, the terms applied to two only have been used constantly since 1878, namely the *Fundatrix* and the *Sexuales*. The term *Sexupara* has been in general use since 1889, but the names given to the other winged, and wingless generations which deposit their eggs on the intermediate host-tree have undergone constant changes.

Mr Steven has again revised the terms for the latter in his paper, and the establishment of the names *Gallicola migrans*, and *Gallicola non-migrans* for the winged forms emerging from Spruce galls, and *Colonici sistens* and *progrediens* for the Larch generations, is admirable.

In the present paper, it is proposed to give a detailed description of the parthenogenetic cycles on the Larch, but for the sake of clarity, a brief summary of Mr Steven's work on the Spruce cycle is recalled.

---

[1] Except in Paul Marchal's paper, *Annales des Sciences naturelles* (*Zoologie*), 9th series, vol. XVIII, 1913, where a few figures of Sexuales of the genus Pineus only are given.

I. THE SPRUCE CYCLE.

The winged *Sexupara*, flying from Larch, lays 5–10 yellow-brown eggs on the older needles of Spruce in June, under a considerable covering of wax-wool.

The male and female *Sexuales* hatching from these moult four times each, and, having reached the adult wingless stage, the female lays a single fertilized egg during the second half of July.

A *Fundatrix* larva hatches from this straw-coloured egg in August, secretes wax-wool and hibernates until the following April. Having moulted three times, the wingless adult *Fundatrix* lays 50–100 eggs under much wax-wool on a weak bud.

These eggs are at first yellow, but later become greenish-brown. Larvae of the *Gallicola migrans* hatch from them, and, together with their *Fundatrix* mother, convert the Spruce bud into a "gall." The larvae undergo three moults within the gall, which opens from the beginning to the middle of July; they emerge as the fourth stage nymph, and a final moult gives the winged adult *Gallicola migrans*, which flies to Larch.

II. THE LARCH CYCLE.

The *Gallicola migrans* lays 20–40 dark brownish-green eggs on a Larch needle, under a very sparse wax-wool covering.

Individuals emerging from a gall on June 14th, 1913, at Oxford, were transferred to young Larch, where they finished ovipositing on June 19th. The larvae hatched from these eggs on July 1st.

A cluster of eggs collected from Larch in Hertfordshire on June 12th, 1919, hatched from June 20th–23rd.

THE COLONICI GENERATIONS.

All larvae hatching from the latter were of the *Sistens* form, and were active at first, but later settled on the bark of shoots and went into hibernation (Plate VI, Fig. 1).

In the following spring the larvae started feeding (Fig. 2), and were observed to undergo the first moult on April 9th, 1914 (Fig. 3), the second on April 15th (Fig. 4), and the third and last on April 20th (Fig. 5). The adult *Sistens* is wingless (Fig. 6) and, according to Mr Steven, lays 5–12 eggs a day, until 35–50 is reached, from March till the middle of May. The eggs are at first yellow, then bronze-green, and hatch into two kinds of larvae, (1) *Progrediens* (Plate VII, Fig. 7) and (2) *Sistens*, the latter being in the minority, and many of them appearing to die soon after hatching. The survivors appear to hibernate.

The *Progrediens* larvae climb onto the Larch needles, and start to suck, causing a bending of the leaf.

After two moults at intervals of seven days (Fig. 8), these larvae become divergent in structure in the third stage, one portion (*a*) remaining elongate and slim (Fig. 9), and the other (*b*) becoming oval and stout (Fig. 12). After a third moult, the former (*a*) become nymphs (Fig. 10), and after a fourth and last, at the beginning of June, the winged adult *Sexuparae* (Fig. 11), which fly to Spruce and produce the *Sexualis* generation. The stout third-stage larvae (*b*) secrete a small amount of wax-wool, then moult for the last (third) time, and become wingless adult *Progredientes* (Fig. 13). These secrete much wax-wool and lay 20–30 brownish eggs, which give rise again to *Progrediens* and *Sistens* larvae: the latter hibernate in the first stage, the former, after two or perhaps three moults, develop to adult *Progredientes*, but no *Sexuparae* are produced from the first or any subsequent *Progrediens* generation. Throughout the summer and autumn, the *Progrediens* generations are continued until the time when the Larches lose their foliage.

Some of the *Progrediens* larvae produced from eggs laid by adult *Sistentes* were kept under observation in Hertfordshire in March and April, 1914, and developed as follows:

	Larvae found on Larch needle	First Moult	Second Moult	Third Moult	Adult oviposited
1.	March 16	March 25	March 29 (wax-wool secreted March 30)	April 2 (much wool secreted)	April 6–14
2.	,, 18	,, 26	March 31 (wool secreted) April 1)	April 5	—
3.	,, 26	,, 30	—	—	—
4.	,, 29	?	April 6 (wool secreted April 8)	,, 14	—
5	,, 29	,, 31	April 2 (wool secreted April 4)	—	—
6.	,, 29	,, 30	April 2 (wool secreted April 4)	,, 8 (much wool secreted)	,, 9–14
7.	,, 29	,, 30	April 2 (wool secreted April 4)	April 8 (much wool secreted)	—
8.	,, 29	?	March 31 (wool secreted April 2)	April 4 (much wool secreted)	,, 6–14

The time from the hatching of the egg to the first moult is therefore about ten days, the second stage lasts from 3–6 days, the third from 5–9 days, and oviposition about ten days.

The fact that wax-wool is secreted by third-stage larvae, two days after the second moult, may possibly have led Mr Steven to believe that only two moults altogether occur in the later *Progrediens* generations; at any rate, the matter is one of little importance, and can easily be cleared up.

III. STATISTICS OF THE COLONICI GENERATIONS.

A. SISTENTES.

The Sistens larvae all hibernate in the first stage, only becoming adult in the spring following; as found in nature, they have a triple origin:

(1) From eggs laid by the *Gallicola migrans*.
(2) From eggs laid by the first generation of Sistens derived from (1).
(3) From eggs laid by the Progredientes of several generations.

In February, 1914, adult Sistentes were observed on Larch in Hertfordshire, and the eggs laid by them collected, to determine the proportion of Progrediens and Sistens larvae hatching from them.

Eggs collected	Eggs hatched	Resulting larvae Progrediens	Sistens
February 19	Feb. 27–March 6	66	0
,, 23	,, 26– ,, 7	60	0
,, 23	March 5– 7	18	0
March 12	,, 16–27	68	0
,,	,, 15–29	90	0
,,	,, 15–26	77	0
,,	,, 16–25	96	0
,,	,, 13–20	144	0
,,	,, 13–20	241	0
,,	,, 13–20	138	0
,,	,, 23–30	45	0
,, 18	April 4–10	76	0
Individual Eggs:			
February 14	February 26–28	6	0
,, 15	March 2–8	13	0
,, 19	,, 30–April 6	10	0
5 egg-clusters collected March 12	,, 12– ,, 10	524	0
	Total	1672	0

During these observations a few of the egg-clusters were kept in a warmed glass-house, the rest outside; in both cases there was a total absence of Sistens larvae. It is noteworthy that Sexupara stages developed, though in small proportions, from these Progrediens larvae.

In May, 1919, the observations were repeated with egg-clusters obtained in the same locality.

Eggs collected	Eggs hatched	Progrediens larvae	Eggs hatched	Sistens larvae	Total
May 17	May 18–27	90	—	0	90
,,	,, 18–27	72	—	0	72
,,	,, 20–June 1	66	—	0	66
,,	,, 18–26	101	—	0	101
,,	,, 18–25	70	May 23–31	38	108
,,	,, 21–26	19	,, 18–31	139	158
,,	,, 21–25	7	,, 18–27	81	88
	Total	425		258	683

It is clear that variation exists from year to year in the proportion of Progrediens and Sistens eggs produced by the adult Sistentes. However, there seems to be some system in this variation.

First, a large proportion of the egg-clusters gave rise only to Progrediens larvae (all in 1914, 4 out of 7 in 1919). Secondly, some clusters produce a very large majority of Sistens larvae, in which case the eggs hatching first in the cluster were Sistens, and *not* Progrediens larvae.

Thirdly, in common with Mr Steven's observations, some clusters produce a majority of Progrediens, and a minority of Sistens larvae, in which case the first eggs hatching gave rise to Progrediens, and only the later ones to Sistens larvae.

As Mr Steven points out, observation extending over many years on isolated trees is necessary to determine with exactitude whether the Sistentes of the three origins produce constant proportions of the two forms, but the above statistics may well point to such research having a definite result, and perhaps even to the trend of that result.

B. PROGREDIENTES.

False proportions are easily obtained if egg-clusters, from which some of the larvae have already hatched and wandered away, are kept under observation.

From seven such clusters collected at Oxford on March 28th, 1914, 17 Progrediens and 25 Sistens larvae hatched between that date and May 18th. In June, 1913, five similar clusters produced 36 Progrediens, and 30 Sistens larvae, between June 14th and June 24th.

These represent the first Progrediens generation, in which the proportions seem to be fairly equal.

The late autumn generations were more closely studied in 1913 at Oxford, and the observations made show that differences of temperature, whether applied to the trees, to the individual insects, or to the eggs during oviposition, probably do not affect the resulting proportions of this generation, and certainly not to any appreciable extent.

Egg-clusters collected 1913	No. of eggs in cluster	Date of hatching 1913	Larvae resulting.		Conditions
			Progrediens	Sistens	
October 19	15	October 22–27	6	4	Natural
November 12	10	November 12–20	9	0	Adult and eggs produced in warm temperature
,, ,,	18	,, 12–25	15	0	do. do.
,, 15	19	,, 19–24	11	4	Natural
,, ,,	15	,, 20–27	6	4	do.
,, 19	25	,, 23–29	25	0	Adult and eggs produced in warm temperature
,, 20	17	,, 24–29	15	0	do. do.
,, 30	28	December 4–10	28	0	Eggs brought into warm temperature after oviposition
,, ,,	22	,, 3–12	22	0	do. do.
,, ,,	26	,, 2–10	8	1 (Dec. 1)	do. do.
,, ,,	12	January 13–22, 1914	12	0	Natural (frost)
,, ,,	24	Nov. 30–Jan. 22, 1914	19	0	Oviposition in warm temperature. Eggs subjected to frost
December 4	5	December 10–12	4	0	Adult and eggs produced in warm temperature
,, ,,	4	,, 12–14	2	0	do. do.
		Total	182	13	

The great preponderance of larvae of the Progrediens type produced by the last generation of the year shows the assumption that only Sistentes hatch from the eggs to be completely false.

It may be noted that a continued exposure to a warm temperature causes a great diminution in the number of eggs laid, and, if climate plays any part at all, this seems to be the only direction in which any effect is produced.

Finally it is suggested that the sap-flow in the plant, and therefore nutrition of the insect in all stages, may well be a prominent determining feature in the production of Progredientes and Sistentes, in addition to the alternative generations from which they may primarily arise.

IV. ECONOMIC CONSIDERATIONS.

A diagram is here given representing every stage in the life-cycle of the Larch Chermes, and modified from that given by C. Börner in 1908, in order to show more accurately the origin and development of the Colonici generations.

The dotted circle in the Spruce cycle denotes the *Gallicola non-migrans* generation, and the Fundatrix generation arising from it, as described by Börner. These generations may occur in Germany, but in Great Britain we have no evidence that they exist, a fact which might modify the most economic means of control considerably.

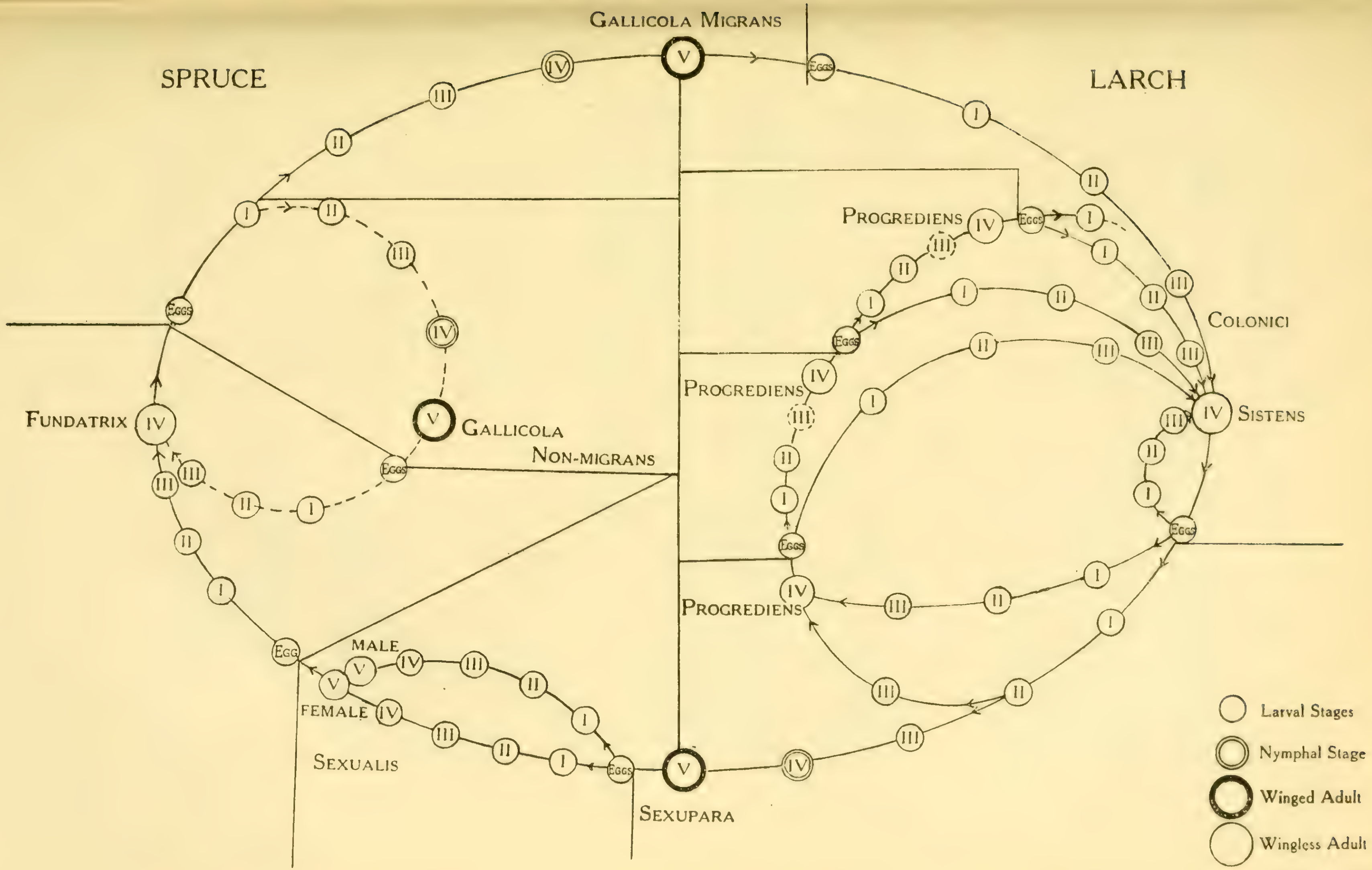
There is no doubt that the brunt of damage is sustained by the Larch in the case of young plants, and Mr Steven has shown that this can be adequately controlled by fumigation.

The Spruce does not appear to be attacked severely while young, and, as applied to Larch, it would certainly seem that a legislative measure is called for, providing for a compulsory fumigation of all Larch trees before planting out in the forest, not only upon the principle of starting with clean stock, but with a view to giving the individual plants a chance to make a good growth from the beginning.

With regard to older Larch trees, it is probable that a good control on the Spruce, growing in the neighbourhood, might well obviate the necessity of a costly and difficult control on Larch, for it now appears that a large majority of the Sistens larvae perish during hibernation, and there is no doubt that the Progrediens generations come to an end with the fall of the leaves, thus accentuating the benefit to be derived if the *Gallicolae migrantes* were prevented from their annual influx from the Spruce.

Except at unwarrantable cost, the galls on the Spruce could hardly be destroyed, and the wintering Fundatrix larvae, with their diffuse distribution over the Spruce buds, and their covering of wax-wool, would present many difficulties if spraying were resorted to. The Sexualis generation, however, is produced, by the Sexupara, on the underside only of the older Spruce needles, during a short period of the summer, and under the wings of the mother insect they remain during their development, only partially covered by an otherwise copious supply of wool, secreted by the parent.

It is the Sexual generation, then, about which least is known, that gives an opening for a method of control by spraying—a remedy rendered economic by the fact that only the underside of the branches need be


GALLICOLA MIGRANS
SPRUCE
LARCH
PROGREDIENS
COLONICI
PROGREDIENS
SISTENS
FUNDATRIX
GALLICOLA
NON-MIGRANS
PROGREDIENS
MALE
FEMALE
SEXUALIS
SEXUPARA
EGGS
EGG
Larval Stages
Nymphal Stage
Winged Adult
Wingless Adult

treated, and perhaps even more so, if it is found that the Sexuparae confine their oviposition only to the lower branches.

The principal economic investigation therefore still lies before us in a detailed study of the habits and structure of the Sexuales, and a determination of the presence or absence of the *Gallicola non-migrans* generation in this country.

Should the latter exist, it probably does so to a very limited degree, and the main control upon the Sexual phase would, in this event, be little disturbed.

V. A METHOD OF PREPARING APHIDAE FOR MICROSCOPIC EXAMINATION.

While investigating the life-history of the Larch Chermes in 1913, it was noticed that ordinary *Sulphuric Ether* had a peculiar effect in "fixing" the chitinous covering of the young stages of this insect, and so of preventing crinkling and distortion.

Later a use was found for this process in the preparation of more advanced stages, both winged and wingless, and in mounting Aphids of considerable size, in addition to insects of other Orders, having extremely delicate chitinous membranes.

Finally, for detailed examination, it was found possible, even with Aphids of considerable bulk, to subject the insects to pressure during Ether-fixation, the resulting *balsam* preparations showing a minimum of distortion, and presenting objects especially suitable for microphotography.

Börner's method for preparing specimens of the Chermesidae in 1908 comprised a preliminary immersion in 70 per cent. Alcohol, and dehydration through 90 per cent. and Absolute Alcohol. The fats were then dissolved out in Sulphuric Ether, and the objects hydrated through Absolute, 90, 70, 50 and 30 per cent. Alcohols, with a final immersion in Distilled water. After clearing in weak Potash, and another immersion in Distilled water, Glycerine was added, and the skins finally mounted in a $\frac{2}{3}$ Glycerine solution.

Roughly this process takes the following time:

	Hours	Minutes
Preliminary Dehydration		15
Fat Dissolution	24	
Hydration		30
Clearing in Potash	6	
Mounting in Glycerine		15
Total	31	

In addition, Börner found it necessary to open the bodies of the larger forms before preparation, so that the method is very long, and glycerine preparations are neither permanent nor very satisfactory.

For quicker, more permanent, and equally satisfactory mounting, the living insect is placed on a glass slide and a cover-glass (large for large objects) is placed over it. A few drops of *Sulphuric Ether* are run beneath the cover-glass, and the ether allowed to evaporate until the pressure of the cover-glass forces out a portion of the contents of the insect; their escape takes place through minute interstices in the chitin of the head, and extremity of the abdomen. For large objects, it is necessary to add a little pressure by means of a needle. The slide is then flooded with Absolute Alcohol, and the cover-glass removed with a fine needle, carefully.

In the majority of cases the object sticks either to the slide or cover-glass, and if sufficiently cleared, as is often the case with small insects, may be mounted in balsam, as described below. The time taken by this process does not exceed 5 minutes.

If, however, clearing with Potash is demanded, the object, after the above treatment with ether and absolute alcohol under the cover-slide, is first hydrated, through the alcohols, into distilled water, cleared in 2 per cent. Potash Solution, and again dehydrated through distilled water to Absolute Alcohol. To the latter, drops of *Turpineol* are added slowly, and finally the object, after immersion in pure Turpineol, is mounted in Canada Balsam (Xylol Solution).

The time taken over this method is roughly as follows:

	Hours	Minutes
Ether-fixation and Hydration		20
Clearing in 2 per cent. Potash Solution	3	
Dehydration		20
Final Clearing in Turpineol and Mounting		5
Total	3	45

The objects, after treatment with ether, are flat, and therefore require considerably less time in dehydration, hydration, and clearing with potash, than in Börner's method.

The final clearing reagents, Clove Oil and Xylol, are unsuitable for these preparations, as distortion and contraction are liable to result, especially after the use of potash. These inconveniences are readily surmounted in their substitution by Turpineol. Chitin-stains, such as "orange," are strongly deprecated.

A number of insects may be treated with the ether on the same slide, and then transferred through Alcohol absolute and 90 per cent. to Alcohol 70 per cent. If any stick to the slide or cover-glass they may be gently removed with a needle, and kept in the Alcohol until time for complete clearing and mounting is available.

It is, however, not advisable, though it is quite possible, to mount more than one specimen under one cover-glass.

The moulted skins of Aphids and other insects lend themselves especially to this mode of preparation, which is justified by the fact that no less than five pairs of delicate glands, not previously described as constant, have made themselves, and the number of their facets, apparent upon the ventral side of the Progrediens larva of the Larch Chermes, immediately after hatching from the egg.

From measurements taken, it would seem that the expansion produced by the pressure on the organism during the process is just compensated for by the contraction which takes place subsequently in dehydration and in the approximation of the dorsal and ventral surfaces, or of the sides, and the insects can be prepared in any position required. Material which has first been preserved in alcohol cannot, of course, be subjected to this process.

The following photographs, except where indicated in one case, have been taken directly from these preparations, and illustrate the stages of the Colonici sistens and progrediens, and the Sexupara, on Larch (*Larix europaea*).

EXPLANATION OF PLATES VI AND VII.

Cnaphalodes strobilobius, Kalt.

Development of Colonici and Sexupara on Larch.

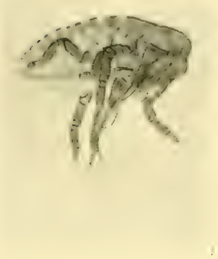
Photographs direct from Preparations. × 50.

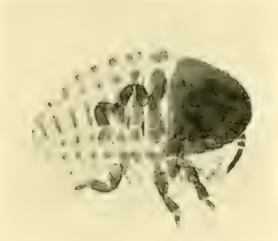
Fig. 1. Sistens. Stage I. Before hibernation.
,, 2. ,, ,, I. After hibernation.
,, 3. ,, ,, II.
,, 4. ,, ,, III.
,, 5. ,, ,, III. Moulted skin.
,, 6. ,, ,, IV. Adult.
,, 7. Progrediens. Stage I.
,, 8. ,, ,, II. Moulted skin.
,, 9. Sexupara. Stage III. Moulted skin.
,, 10. ,, ,, IV. Nymph.
,, 11. ,, ,, V. Adult.
,, 12. Progrediens. Stage III.
,, 13. ,, ,, IV. Adult.

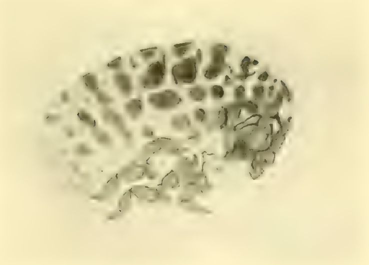
Fig. 1. Potash-glycerine preparation.

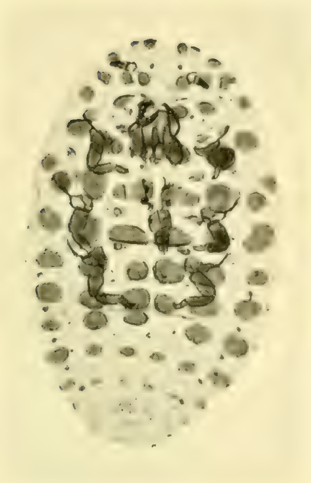
Figs. 2–13. Ether-potash-balsam preparations.

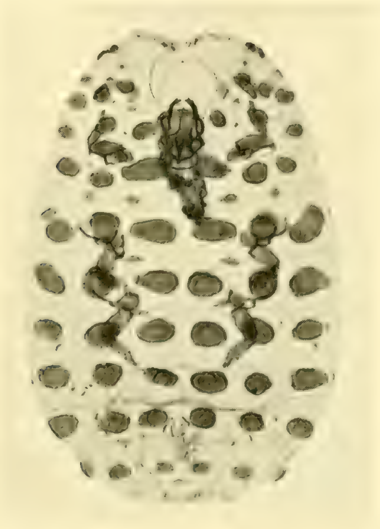
Figs. 1–7, 10, 11, and 13 from photographs taken by Messrs W. Watson and Sons, 313 High Holborn, London.

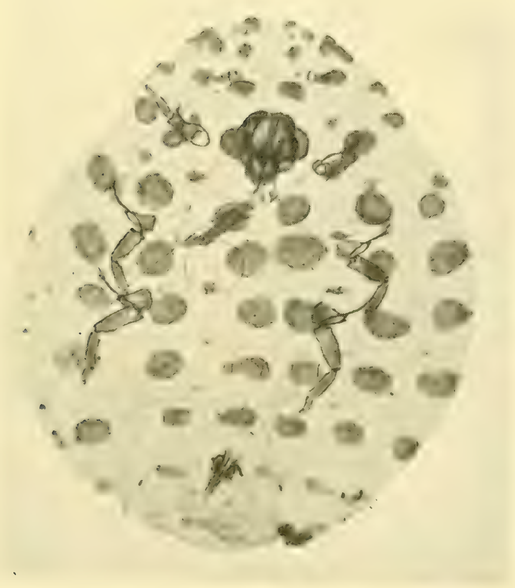

1

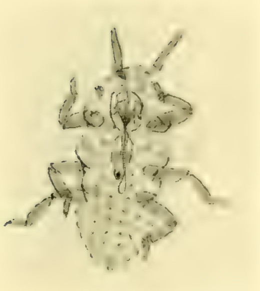

2


3

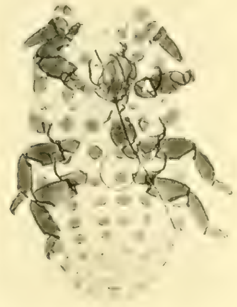

4


5

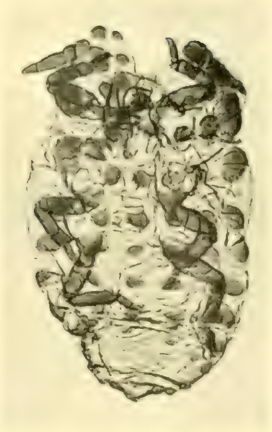

6



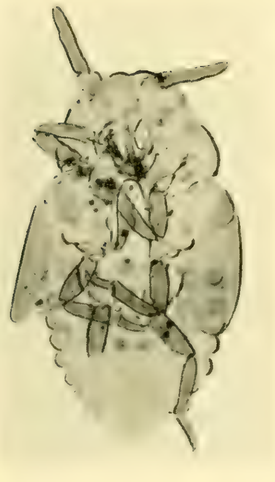
7



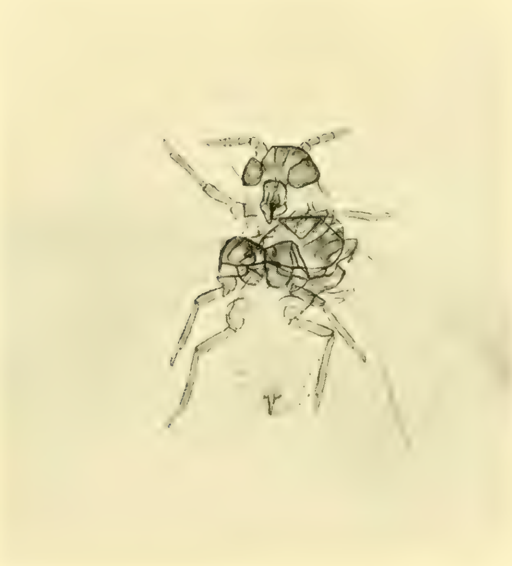
8



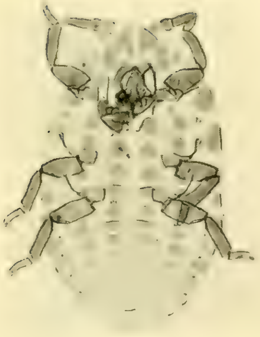
9



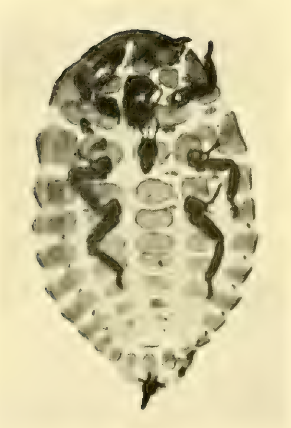
10



11



12



13

STUDIES IN BACTERIOSIS. IV.—"STRIPE" DISEASE OF TOMATO.

By SYDNEY G. PAINE

(*Lecturer in the Department of Plant Physiology and Pathology of the Imperial College of Science and Technology, London*)

AND

W. F. BEWLEY

(*Mycologist at the Experimental and Research Station, Cheshunt, Herts.*)

(With 5 Text-figures and Plates VIII and IX.)

INTRODUCTION.

The disease of tomatoes known to the nurseryman as "Stripe" is characterised by brown longitudinal markings or stripes on the stem, by shrivelling of the leaves, and by sunken irregularly shaped pits usually of a brown colour on the fruit. It is a specific communicable disease due to a bacillus which has previously been described as the cause of a very similar disease of the sweet pea.

So far little is known concerning the geographical distribution of the disease. It is very common on tomatoes grown under glass in this country and in the Channel Islands. There is no doubt that it occurs also in parts of Canada and the United States. Howitt and Stone(2) have given a description of a tomato disease occurring in Ontario and Pennsylvania, which agrees exactly with that here described. These workers, however, failed to obtain any causal organism and believe their disease to be due to some chemical or physical deficiency in the soil. Bailey(1) in 1892 and Selby(7) in 1897 both seem to have had this disease before them.

In many cases the disease is not of a very serious nature, by most nurserymen it is regarded rather as a nuisance than as a disastrous pest for, with care, a moderate crop of fruit can be obtained from plants which have been attacked. At times, however, the disease may be so prevalent as to ruin the whole crop.

INCIDENCE OF THE DISEASE.

Sometimes, during the first years of a nursery, plants have shown a considerable amount of disease, but this has gradually diminished until only a small percentage of the plants have been attacked in the later years. Conversely, cases are known where "Stripe" has appeared and gradually increased after some ten or twelve years during which time no sign of the disease has been observed. These facts would seem to indicate the soil as the main source of infection and Howitt and Stone(2) have shown that plants grown in soil from an infected house developed the disease while plants grown in the same soil previously sterilised remained free. The disease may appear in the seed-boxes, producing rapid destruction of the young plants and compelling fresh sowings to be made; it is not uncommon to find the first symptoms of disease while the young plants are still in the small pots (sixties) or again after these have been planted out in the houses for a fortnight or so. Usually, however, the disease first appears about May, when the earliest fruit is ready for picking, but frequently no signs appear until the tops are allowed to develop, when these often become badly attacked.

There is a distinct connection between soft and rapid growth and the incidence of disease, plants growing rapidly in the early stages are more liable to "Stripe" than others of a hardier nature. In one case observed at Cheshunt the plants were so badly attacked that it seemed impossible for the crop to recover, the conditions were then altered so as to induce a slower rate of growth with the result that the plants completely "grew out of" the "striped" condition, showed perfectly clean tops and yielded a good crop of sound fruit.

OBSERVATIONS ON THE EXPERIMENTAL PLOTS.

During the past season observations have been made on the manurial plots in the houses at Cheshunt to ascertain the relation of manurial treatment to the incidence of the disease. The indications are that a soft rapid growth such as is produced by excess of nitrogen and a high temperature accompanied by damping renders the plant more susceptible to stripe than does a hard slow growth accompanied by suitable additions of potash.

These observations are fully confirmed by inoculation tests carried out on plants grown in pots, the results of which will be found under the heading "Inoculation Experiments."

The effect of different manurial treatments on the incidence of stripe.

Variety	Treatment	Total No. of plants	No. of diseased plants
Comet	*C.A. without potash	120	78
,,	Control untreated	120	50
,,	C.A. with dung	120	45
,,	C.A. without Phosphates	120	41
,,	C.A.	120	40
,,	C.A. without nitrogen	120	34
,,	Double C.A.	120	34
Kondine Red	C.A. without potash	120	33
,,	C.A. with dung	120	33
,,	Control untreated	120	30
,,	C.A. without phosphates	120	28
,,	C.A. without nitrogen	120	19
,,	Double C.A.	120	14
,,	C.A.	120	13

* C.A. = complete artificials.

The effect of "damping" on the incidence of the disease.

	Damped		Not damped	
Variety	Total plants	No. striped	Total plants	No. striped
Comet	260	124	260	110
Fillbasket	260	112	260	95
Kondine Red	260	112	260	82
Ailsa Craig	260	95	260	34

The effect of forced and slow growth on the incidence of the disease.

	Forced growth		Slow growth	
Variety	Total No. of plants	No. of diseased plants	Total No. of plants	No. of diseased plants
Fillbasket	100	58	100	44
Comet	100	38	100	26
Kondine Red	100	24	100	14
Ailsa Craig	100	24	100	16

Besides showing the effect of manurial treatment and of forcing conditions these tables bring out clearly marked differences in the relative susceptibility of the varieties tested and point to the selection or breeding of a resistant variety as one means of controlling the disease.

THE MODE OF INFECTION.

As stated above the most usual mode of infection would appear to take place underground; young attacked plants show on examination a brown discoloration of the root cortex (Fig. 1). The frequent occurrence of disease in the seed-bed suggests that the seed from infected fruit may also be infected or carry the causal organism externally though so far no actual proof of this has been obtained. Observations in nurseries and practical experiments have shown that the disease may sometimes spread downwards; successful "prick" inoculations have been made on the upper parts of plants and indicate that insects may produce infection of these parts. It is also fairly certain that the pruning knife is a potent factor in spreading the disease; in one house it was observed that disease had spread from one end on both sides of the house while in another it had spread a certain distance down one side only, in the former case it was shown that the pruning had been across the house from left to right, while in the latter the pruning had been down one side and up the other.

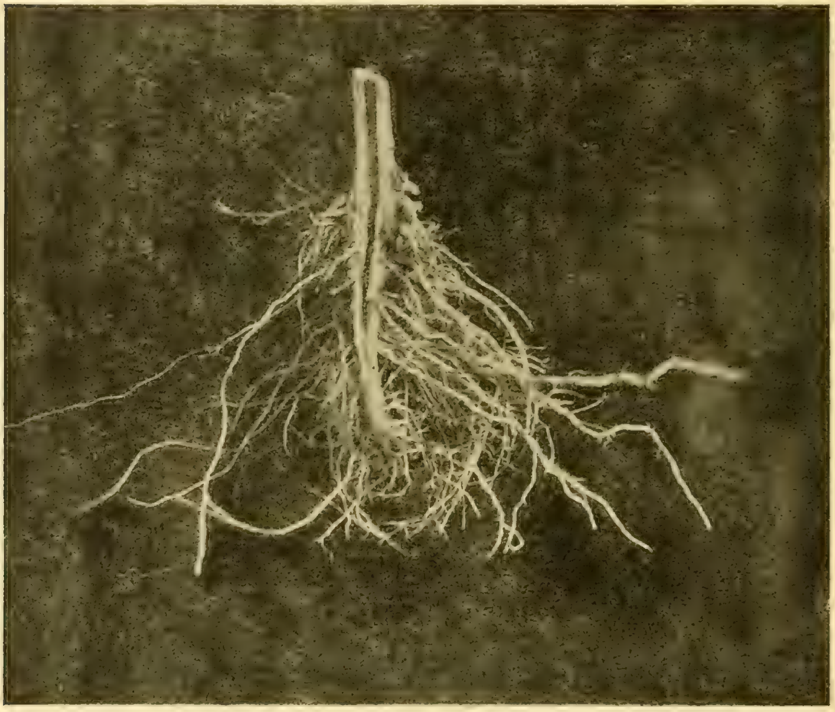


Fig. 1. Showing brown stripe on the root of a tomato plant affected with "Stripe Disease."

SYMPTOMS OF THE DISEASE.

The stem of an attacked plant shows the earliest symptoms of disease as light or dark brown to black sunken patches of irregular shape, varying from small spots to long furrows and "blazes"; the blazes are often three or more inches long and frequently extend over the entire length of an internode. They are well shown in the photograph, Plate IX, fig. 1. In slight cases these markings occur intermittently along the stem while in bad cases the typical furrows can be found throughout the whole length of the stem and on the leaf and truss stalks. The name "Stripe" aptly describes this distinctive feature of the disease, but it should not be confused with the "Black Stripe" supposed to be due to *Macrosporium solani*[1].

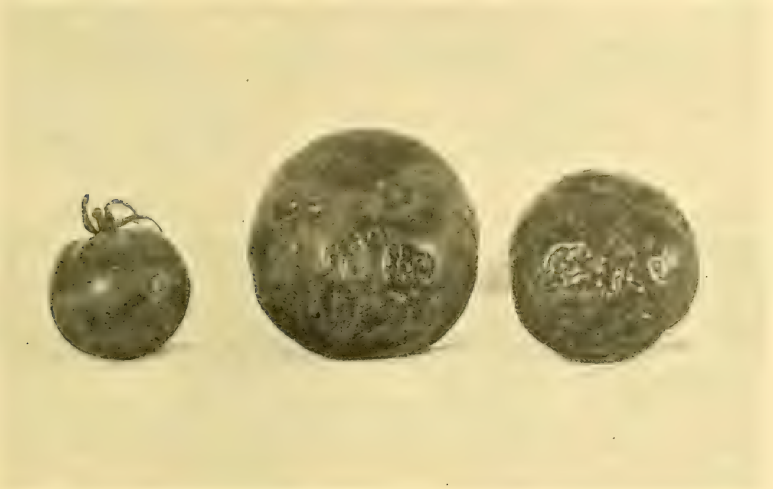


Fig. 2. Showing ripe fruits of tomato infected with "Stripe Disease."

On the leaf the disease first appears as yellow blotches near the mid-rib and the main veins. These later turn brown and extend so that finally the greater part of the surface becomes browned and much distorted by the shrivelling of the diseased areas.

The fruits show light or dark brown sunken patches with round or irregular outline well shown in Figure 2, Plate VIII and Plate IX, figs. 4

---

[1] There is however considerable doubt whether this is a distinct disease. It seems highly probable that *Macrosporium solani* exists as a saprophyte upon the tissue destroyed by the "Stripe" bacillus. This is emphasised by the fact that W. Dyke (quoted by "W" in *Gard. Chron.* 51, p. 52, 1912) thought that this fungus was the cause of Streak Disease of Sweet Peas, a disease now known to be due to a bacillus.

and 5. They vary from a few spots developed near the calyx to many scattered promiscuously over the surface of the fruit. They greatly reduce the market value and in bad cases, as in Plate VIII, the fruit is rendered quite unsaleable, being almost covered with these pock-like depressions.

Attacked plants become very brittle and are easily broken by the workers. In the worst case the whole plant becomes covered with lesions and finally dies.

MORBID ANATOMY.

Lesions in the pith and cortex are the characteristic internal features of the disease, the walls of the attacked tissues are strongly browned so that the patches are readily seen on splitting the stem with a knife. Plate IX, fig. 2 shows rather advanced lesions in the pith of a stem and fig. 1 shows a typical lesion in the cut petiole. In older stems which have become hollow, small brown patches occur in the remains of the pith and in the cortex but at the nodes where the pith is close and moist the patches are much larger. Microscopic examination of the stem seldom reveals the presence of the parasite in a living condition in these patches, but the walls stain deeply with fuchsin and the intercellular spaces are choked with deeply staining material strongly indicating bacterial attack. The appearance of the diseased tissue is not that of a soft rot though the middle lamella is partially destroyed. The cells appear to be torn asunder by shrinkage of the dead cells and tension set up by growth of the surrounding healthy tissue (see Fig. 3): eventually large cavities are produced in this way.

The roots are often found to be diseased only in the upper portion and infection can usually be traced to some wound or insect puncture just below the ground level; the tissues of the lower roots are in these cases white and apparently healthy. In some cases, however, no wound can be discovered, but the cortex is found to be browned to a considerable depth below the soil level and microscopic examination shows the presence of the bacillus in the tissue. It seems that penetration of the root may occur without the aid of a wound, but of course there is always the possibility that a small wound has escaped observation or again that the disease has spread down to the root from an aerial infection.

From the root the organism travels up the stem in the peripheral parts of the pith next to the proto-xylem elements. The organism is very seldom found within the wood vessels themselves, and for some considerable time despite careful examination one could not demonstrate the passage of the organism through the vascular cylinder to the cortex, where it produces the typical lesions or external stripes. Ultimately, however, the process was made clear by a series of transverse and longitudinal sections. The bacilli work outwards towards the parenchymatous elements of the wood or the medullary rays, the cell-walls

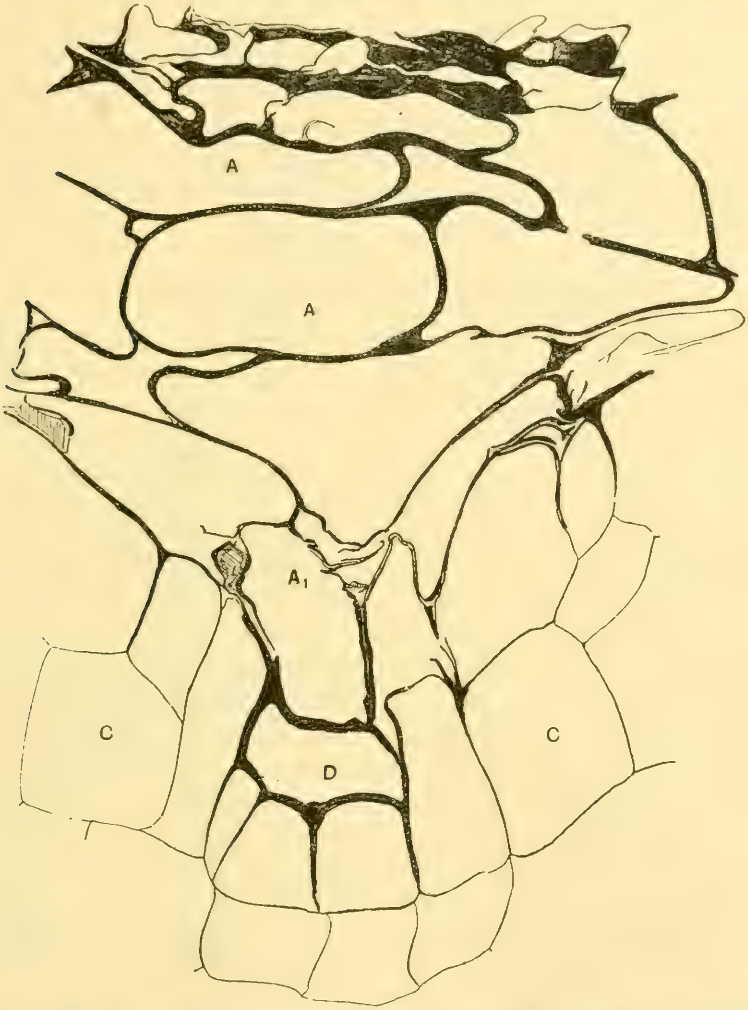


Fig. 3. Transverse section of a Striped stem through the browned region of the cortex. The black masses indicate the attacked cell-walls which harbour the bacteria. *A*. The distorted cells of the collenchyma. A_1. Collenchyma cells showing the destruction of the middle lamella. *C*. Healthy cortex cells. *D*. Attacked cortex cells.

become swollen and browned, and the middle lamella is destroyed, thus opening up a passage for the organism (see Fig. 4). The wood parenchyma is distorted and browned and occasionally the wood vessels themselves are attacked and their walls disintegrated. Once through the vascular region the organism readily finds its way through the cortex to the exterior where it spreads upwards in the outer cortical layers and epidermis; the affected cortical cells collapse and the characteristic depressed stripe is thus produced on the surface of the stem. Anatomical examination of artificially infected plants has fully confirmed the conclusions drawn from naturally infected stems.

ISOLATION OF THE CAUSAL ORGANISM[1].

The organism was first isolated in September, 1918, from plants grown under glass without artificial heat. The plants were badly attacked when first observed and the crop of that house was an entire failure. Sections of the stems showed no sign of active bacteria and several attempts to isolate the organism from the stem proved abortive. In one instance out of perhaps twenty attempts a yellow organism in company with others was obtained on plating from the diseased pith and this afterwards proved identical with an organism which was much more readily obtained from diseased patches on the fruits. Many of these fruit spots seemed to be sterile and frequently on incubation of a diseased fruit the disease failed to extend further. It must be concluded that the organism which had given rise to these diseased patches was no longer viable. A similar case of the disappearance of a plant parasite in diseased tissue has been briefly described in the disease named by one of us (Paine (5)), the Internal Disease of the Potato, and has been suspected by the same author in a Leaf Spot Disease of *Protea* (6). It is quite probable that *bacteriolysis* in plant tissues is a more common phenomenon than it is at present believed to be. This may account for the fact that Howitt and Stone (2) and the four well-known bacteriologists to whom they submitted diseased plants failed to isolate any causal organism from tomatoes bearing exactly the same symptoms as are associated with our "Stripe."

The organism can often be seen in the intercellular spaces of sections of diseased tissue from a fruit spot, and platings made from such tissue

---

[1] The joint authors of this paper isolated the same organism independently and finding they were studying the same disease agreed to collaborate. The cultural work has been carried out by the first-named author at the Imperial College, while the other is responsible for the inoculation experiments which have been conducted at Cheshunt.

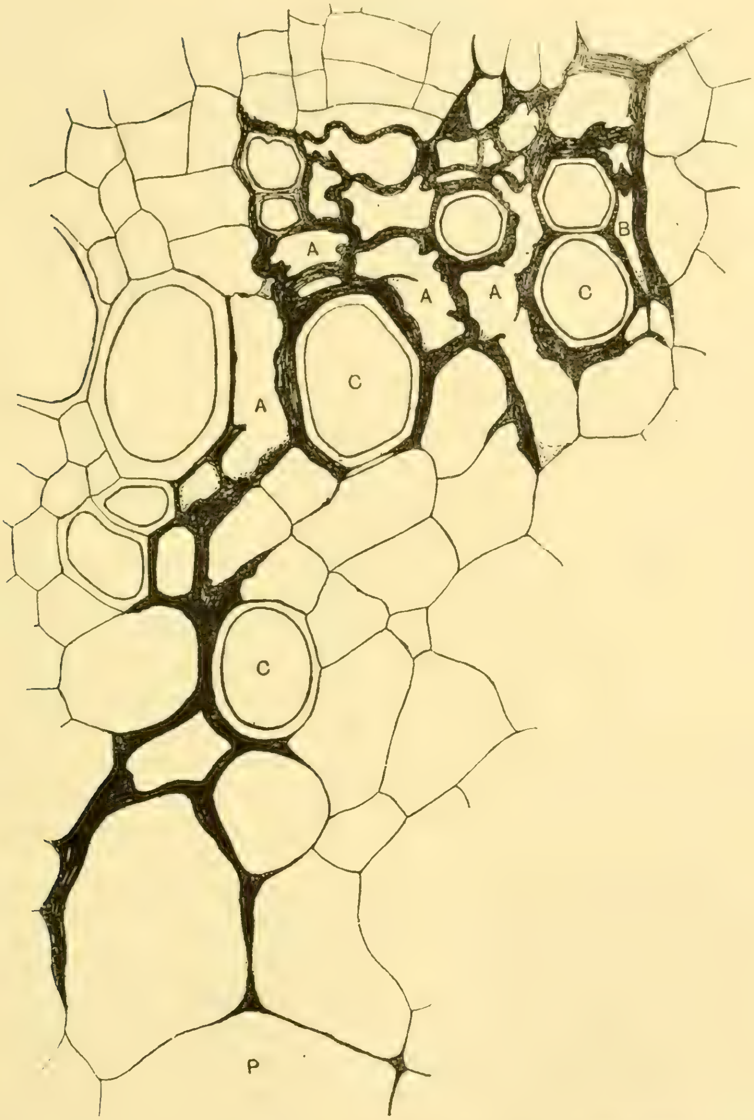


Fig. 4. Transverse section through the vascular bundle showing the passage of the organism from the cortex to the pith. *A.* The wood parenchymatous cells undergoing disintegration by the organism. *B.* Cavity left by the destruction of the middle lamella. *C.* Wood vessels. *P.* Pith.

have often yielded pure cultures without difficulty. On two occasions, from a fruit and a stem respectively a distinctly different organism was found in great preponderance and in fact in almost pure condition. This organism caused no disease when inoculated into plants; it is briefly described below since it agrees in all its characters with *Aplanobacter michiganense,* which has been described by Smith (8) as the cause of a disease in tomatoes.

DESCRIPTION OF THE CAUSAL ORGANISM.

A. MORPHOLOGICAL CHARACTERS.

The organism is a small yellow oval rod measuring from $1{\cdot}2\mu$ to $2{\cdot}0\mu$ in length and $0{\cdot}8\mu$ to $1{\cdot}0\mu$ in width; pairs are not common but are found up to $3{\cdot}4\mu$ in length. These measurements were made on a preparation from a broth culture incubated 24 hours at 22° C. fixed in formalin and stained with aqueous methyl violet.

It is a motile organism with peritrichous flagella usually from four to six in number and from four to ten micra in length. The flagella stain well by the method of van Ermengem (see Fig. 5). The organism rapidly comes to rest when grown on solid media, sometimes within 24 hours, but remains motile for three or four weeks in broth cultures. Examined in water suspension under a cover-glass the motion is of the "free swimming" type with frequent spells of "tumbling" on the short axis. At the centre of the cover-glass the motion slows down considerably after half-an-hour, but continues for upwards of three-quarters of an hour to one hour.

Staining capacity. The bacillus stains readily with carbol fuchsin, Victoria blue and methyl violet. It is gram negative.

Capsules. The presence of a capsule has been suspected round organisms forming a ring at the surface of broth cultures and in cultures in Uschinsky solution. They could not be seen under dark-ground illumination and it has not been possible to demonstrate them by staining. Films from Uschinsky solution stained with gentian violet frequently show a clear halo around each organism and the distribution of the organisms in a crowded film is what one would expect for a capsulated organism, *i.e.* the stained rods are never actually in contact with one another. If a capsule is present it is not a very wide one and does not stain by the usual methods employed for capsule staining.

B. CULTURAL CHARACTERS.

In all cases, unless otherwise stated, the incubation temperature has been 22° C.

Plate cultures in bouillon agar + 10. The colonies on poured plates show after 24 hours; surface colonies have a diameter of ½ to 1 mm., depth colonies are lenticular and just visible with a lens. The surface colonies are round, raised, wet-shining, with a tendency to excentric development from a depth colony. The colour is a mid-chrome by reflected and somewhat milky by transmitted light.

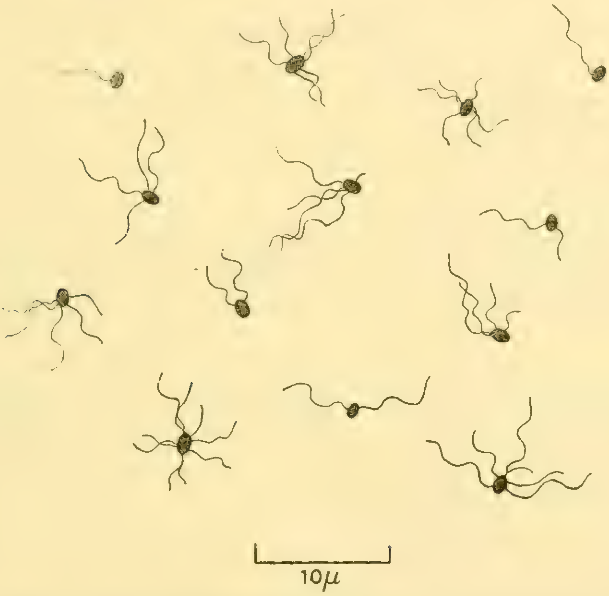


Fig. 5. Showing *Bacillus lathyri* stained by Steven's modification of van Ermengem's method.

Streak cultures on bouillon agar + 10. The streak is raised, wet-shining, butyrous yellow, with entire margin.

Stab cultures on bouillon agar + 10. Growth is visible along the stab after two days as a narrow yellow streak right to the bottom of the stab. The margin is slightly echinate. The surface colony after five days has a diameter of 4 mm. and a bright yellow butyrous appearance.

Plate cultures on bouillon-gelatine + 10. Colonies appear on the second day, are 2 or 3 mm. in diameter on the third day, and show no sign of liquefaction for 8–10 days. A liquid halo then appears and eventually after some three weeks a liquid basin is formed with a yellow granular precipitate at the bottom.

Stab culture on bouillon-gelatine + 10. Growth was visible after 48 hours. On the third day there was no liquefaction, the margin of the stab was echinate and that of the surface colony smooth and round. There was still no liquefaction on the seventh day. The tubes were then taken from the incubator and when examined a fortnight later liquefaction had commenced at the top. Liquefaction was very slowly produced and even after six weeks only the upper portion of the stab had become saccate. A granular yellow precipitate had collected at the bottom of the liquid portion.

Cultivation on other media. The organism grows well on media of many plant extracts. Especially well on potato-mush-agar, on "Marmite" (yeast extract) agar and in milk. Good growth was also obtained on cabbage and celery agar. The most favourable reaction appears to be about + 5 of Fuller's scale. The limits of tolerance towards alkali were not determined.

Streak culture on cooked potato. Growth was apparent after 24 hours. On the second day the streak was 3 mm. wide, bright yellow, raised and butyrous. No stain was produced in the surrounding potato tissue.

Thermal death point. Tubes of bouillon were immersed in a thermostat at 45°, 47°, 49°, 51°, 53°, and 55° C. The hot broth was inoculated with a loopful of a bouillon culture 24 hours old and left in the bath for 10 minutes at each temperature. On subsequent incubation those heated above 51° C. failed to become turbid.

C. PHYSIOLOGICAL CHARACTERS.

For the following tests a 48-hours agar culture was used to inoculate the tubes and the incubation temperature was 22° C. The strains isolated independently by the two authors were set up in parallel and always produced identical results.

10 *per cent. peptone* + 2 *per cent. glucose.* The colour of the litmus became faintly red on the second day, a ring had formed and a loose pellicle, but no gas. On the seventh day the acidity was not much more marked, the colour was slightly redder than the control, no pellicle formed but a decided ring; a very small bubble of gas had collected in the Durham's tube, it had not a greater volume than that occupied by the head of a match and later became almost entirely dissolved. The colour remained practically of a neutral tint for some time and finally

only brown. On titration after two months' incubation the original 10 cc. required 1·3 cc. of $\frac{N}{10}$. NaOH for neutralisation against phenolphthalein as against 1·0 cc. required by the control. This small degree of acidity and small development of gas were consistently observed but they do not appear to justify the classification of the organism as a glucose fermenter. They possibly arose from some impurity in the sample of peptone employed although a control tube of peptone without sugar did not give this result. The organism was still motile in the brown broth when examined after 26 days.

10 *per cent. peptone* + 2 *per cent. lactose.* The colour remained neutral. A strong ring formed but no pellicle.

10 *per cent. peptone* + 2 *per cent. sucrose.* Precisely the same as in case of glucose above.

Bouillon + 2 *per cent. mannite.* Became acid on the fifth day. No gas formed.

Bouillon + 1 *per cent. nitrate.* Slightly turbid on the first day and nitrite was present. On the second day the nitrite was strongly positive and remained so for two months. Turbidity was never very strong, no ring or pellicle was produced but the broth became somewhat mucoid.

Potato plug. About 1 cc. volume of the plug taken from half-way down ground in 200 cc. of water on addition of 1 cc. of iodine gave a bright red colour, no trace of starch remained. Diastatic action is therefore strong.

Uschinsky solution. Distinctly turbid on the second day, a ring had formed and the colour was neutral. On the fifth day the litmus had begun to bleach, a strong yellow ring had formed and a loose pellicle which was easily broken up. After twenty days the litmus had become completely bleached, a strong yellow ring and pellicle were formed and a large yellow deposit filled the lower half of the tube. This was very mucus-like and spread on a slide almost like a sputum. As stated above capsules were suspected to be present, especially in the yellow ring, although no demonstration of a capsule could be obtained.

Dunham's solution. Became turbid on the second day, a loose yellow pellicle formed later. Indol was tested for on the thirteenth day but was not present.

RELATIONSHIP OF THE CAUSAL ORGANISM.

Comparison of the above characters with those of other plant parasites leads to the conclusion that the organism here described is closely related to, if not identical with, *Bacillus lathyri* found by Manns and Taubenhaus (4) as the cause of diseases of the sweet pea, red clover and soya bean, etc. A full description of this organism published by Manns (3) shows close agreement with the above. Noteworthy points of similarity are: (1) the morphology; the position of the flagella being rather unusual for a bacillus, they are certainly peritrichous but there is a marked tendency for those at the anterior end to be lacking in stained preparations (see Fig. 5); (2) the butyrous and viscid growth on most solid media; (3) the mucoid development in fluid media, especially in Uschinsky solution; (4) the slow liquefaction of gelatine; (5) the effect in litmus milk. Only two points of difference appear: (1) in the resistance to heat; *B. lathyri* has a thermal death point of 48° C. and shows no growth at 37½° C. whereas the "Stripe" organism has a thermal death point of 51° C. and does grow, though very sparingly, at 37—38° C. It is quite conceivable that continued existence at the temperature of the forcing house may have raised the heat-resisting power of the strain; (2) in the power to reduce nitrates; Manns found no reduction of nitrate by *B. lathyri* though in this connection he states "Several of the strains produce nitrites from peptone broth; thus in nitrate broth unless quantitative determination is made for the nitrates placed therein one might easily assume nitrate reduction." Special care was therefore exercised in determining the reducing power of the "Stripe" organism. Pure strains from three separate isolations of the organism were inoculated each into six tubes of beef extract ("Jardox") with, and six tubes without, the addition of 1 per cent. potassium nitrate. After incubation for three days all the eighteen tubes containing nitrate gave positive reactions for nitrite while the eighteen controls without nitrate gave negative results. Nitrite was shown by azo-colour formation in the sulphanilic acid + α naphthylamine reagent. This is a very delicate test for the presence of nitrite and is probably more reliable than the method of determination of nitrate adopted by Manns.

The crucial test of identity will be the cross-inoculability of the "Stripe" organism from the tomato to the sweet pea[1]. This has not been attempted as yet for the reason that the identity of the organism with *B. lathyri* was only discovered after this paper had been sent to the press. Experiments to settle this point will be made next summer.

---

[1] In this connection it is noteworthy that Manns has isolated *B. lathyri* from tomatoes showing Blossom-End Rot and has been able to produce the symptoms of this disease by artificial infection of tomatoes with a strain of *B. lathyri* isolated from a species of *Lathyrus*.

INOCULATION EXPERIMENTS.

Preliminary Experiments.

28. 5. 19. Six young tomato plants (Comet variety) were used. The stems were washed with alcohol and then with sterile water. A small piece of culture was pricked in near the top of the plant and the wound covered with tin-foil to avoid secondary infection.

31. 5. 19. Brown corky patches appeared round the stab.

11. 6. 19. Black furrows up and down the stem from the stab. Three inches up and two down.

28. 6. 19. Typical black furrows on the stem up and down from the wound. Leaves browned in patches. General appearance of striped plants.

Three controls were perfectly healthy.

28. 5. 19. Six young plants as in the previous experiment were used. Inoculations were made by pricking in a piece of culture near the base of the plant and covering as before.

14. 6. 19. Black furrows eight inches up the stem. Lower pair of leaves attacked.

30. 6. 19. Plants smothered in lesions.

Three controls were perfectly healthy.

28. 5. 19. Six plants removed from the soil and their roots well washed. They were then washed in alcohol followed by sterile water. They were inoculated by rubbing a piece of culture on the roots, and were then re-planted.

15. 6. 19. First brown patch appeared on the stem about half an inch above the soil level.

29. 6. 19. Lesions on the stem seven inches from the ground.

5. 7. 19. Plants badly attacked.

Three controls quite healthy.

5 7. 19. Organism re-isolated from representative members of each experiment.

3. 6. 19. Four plants two feet high were inoculated by rubbing a piece of culture on a rough leaf-base such as is left by careless pruning.

8. 6. 19. Bases blackened and furrows appear which run from the base to the stem.

15. 6. 19. Furrows down the stem two inches below the inoculated base.

3. 7. 19. Furrows up and down the stem. First and second pair of leaves above and the first pair below the point of inoculation attacked. Two controls healthy.

3. 6. 19. Four plants two feet high were used. Several badly striped leaves were crushed in a mortar and the juice rubbed into a carelessly pruned leaf-base.

11. 6. 19. Bases blackened.

30. 6. 19. Typical stripe furrows running from the bases into the stem were visible.

21. 7. 19. The plants were all badly striped.

Four controls made by rubbing the juice of healthy leaves into jagged leaf-bases were perfectly healthy.

3. 6. 19. Four green tomato fruits were inoculated by pricking in a small piece of culture after sterilising the outside.

10. 6. 19. Brown ring round the prick.

17. 6. 19. Brown sunken patch round the prick. The fruit was cut open when it was found that the tissue round the stab was browned. A brown patch was present in the loculus wall, from which the organism was re-isolated.

The control fruit showed the wound healed and no sign of stripe.

20. 7. 19. The organism re-isolated from inoculated plant on 5. 7. 19 was pricked into six twelve inch plants.

29. 7. 19. Typical furrows on stem near the wound.

1. 8. 19. The organism was again isolated and found to be identical with the original.

The effect of manuring upon the results of artificial infection.

A standard soil compost was made up as follows:

72 cubic feet of virgin soil,
32 lbs. lime,
8 ,, bone meal,
8 ,, bone flour.

72 twelve inch pots were each given one cubic foot of the compost. To these pots nitrogen in the form of ground hoofs and potash as sulphate of potash were added in varying amounts. Each series consisted of eight pots planted with uniform tomato plants of the variety Comet.

Series 1.	1 c. ft. compost and	$\frac{1}{9}$	lb.	hoofs per pot		No potash
,, 2.	1 ,, ,,	$\frac{2}{9}$	,,	,, ,,		
,, 3.	1 ,, ,,	$\frac{3}{9}$	,,	,, ,,		
,, 4.	1 ,, ,,	$\frac{1}{9}$	,,	K_2SO_4 ,,		No nitrogen
,, 5.	1 ,, ,,	$\frac{2}{9}$	,,	,, ,,		
,, 6.	1 ,, ,,	$\frac{3}{9}$	,,	,, ,,		
,, 7.	1 ,, ,,	$\frac{1}{9}$	,,	hoofs and	$\frac{1}{9}$ lb. K_2SO_4 per pot	Complete
,, 8.	1 ,, ,,	$\frac{2}{9}$	,,	,, ,,	$\frac{2}{9}$,, ,, ,,	
,, 9.	1 ,, ,,	$\frac{3}{9}$	,,	,, ,,	$\frac{3}{9}$,, ,, ,,	

28. 5. 19. Six plants of each series were inoculated by "pricking in" some of the culture into the lower portion of the stem and covering the wound with a piece of tin-foil to prevent secondary infection. Two plants of each series were left as controls. They were pricked with a sterile needle and covered in the usual way.

Series 1.

31. 5. 19. Brown corky appearance round the stab.

12. 6. 19. First pair of leaves above the wound showed typical stripe lesions. Furrows three inches up the stem.

20. 6. 19. Plant typically striped two feet up the stem.

Series 2.

31. 5. 19. Lesions round the "prick" more distinct than in Series 1.

12. 6. 19. Furrows nine inches up the stem.

20. 6. 19. Lesions more advanced than in Series 1.

Series 3.

31. 5. 19. Discoloration still more intense than in Series 2.

12. 6. 19. Furrows up the stem eleven inches.

20. 6. 19. Five out of the six plants showed lesions in the tops. The sixth one had the top seven inches clean.

Series 4.

31. 5. 19. Slight discoloration round the "prick."

12. 6. 19. Furrows two inches up the stem from the wound.

20. 6. 19. Very little stripe on four plants, but two showed lesions on the first pair of leaves above the wound.

Series 5.

20. 6. 19. Very little stripe showing on any plant.

Series 6.

No stripe at all, except in one case where the plant had rooted through the pot into the rich soil beneath.

Series 7.

Similar appearance to plants in Series 1.

Series 8.

Similar to Series 1.

Series 9.

12. 6. 19. Like Series 2. Furrows up to three inches above the wound.

20. 6. 19. Third pair of leaves above the wound attacked.

All controls healthy.

21. 8. 19. The preceding experiment was repeated with precisely the same results. The indications were that increasing amounts of nitrogen without potash produced an increasing susceptibility to the disease, while increasing amounts of potash without nitrogen gave a corresponding increase in resistance to it. Where potash and nitrogen were used together there were indications that the potash counteracted the effect of the nitrogen.

CONTROL OF THE DISEASE.

Several methods are suggested:

(1) Sterilisation of the soil by heat.

(2) Sterilisation of the seed by means of formaline.

(3) Selection of resistant varieties.

(4) Sterilisation of the pruning knife in cases where the disease has been noticed, especially while pruning the diseased plant and before passing from the diseased plant to healthy ones. This might easily be effected by wiping the blade of the knife with a rag soaked in 2 per cent. lysol or some similar disinfectant. The prunings from diseased plants should not be thrown to the ground but carefully collected and burnt.

(5) The cutting away of a diseased stem and allowing a lateral to develop will often give a clean plant.

(6) Care in the use of artificials to see that potash is present in sufficient quantity and nitrogen not inordinately abundant.

COMPARISON OF THE STRIPE DISEASE WITH THE GRAND RAPIDS TOMATO DISEASE.

The Grand Rapids Disease has been investigated by Smith (8) and attributed to a bacterium which he has named *Aplanobacter michiganense*. It has been stated earlier that an organism was isolated from "Striped" plants which seems to agree closely with *A. michiganense*. The organism is a small oval non-motile rod, gram positive, growing well on neutral or slightly acid media forming a very viscid, deep orange-coloured slime, so viscid in fact that, when the culture is young, difficulty is experienced in lifting any of the slime on a platinum wire. In old cultures this difficulty is not so great. The colour of litmus milk remains unchanged for 10 days to 14 days at 22° C. and a thick deep yellow mucilaginous ring and pellicle form at the surface, the casein is not coagulated but becomes slowly digested; at the end of a month the whey is quite clear and red, and a precipitate containing tyrosine crystals is found at the bottom of the tube. In untinted milk the yellow ring is again the only noticeable change during the first fortnight, after which the casein is digested slowly without coagulation and the whey becomes quite clear and bright yellow in colour. Nitrates are not reduced, slight turbidity is formed in the nitrate broth but no ring or pellicle is produced, in three days at 22° C. the broth becomes very mucus-like and the organism is found in short chains appearing almost like a *streptococcus*, except that the component cells are oval in shape. Dunham's solution became slightly turbid and mucus-like, indol was produced.

No growth was observed in 10 per cent. peptone containing 2 per cent. of glucose, lactose or saccharose and the colour of the litmus remained unchanged even after a month in the incubator. No growth was obtained in Uschinsky solution.

A comparison of these reactions with those described by Smith for

Aplanobacter michiganense make it at least probable that the two organisms are identical. But whereas Smith claims to have made repeated successful inoculations with his organism and has stated that virulence is retained for some months in artificial cultures the organism here described has not shown any sign of parasitism, although repeated attempts at infection have been made, the earliest being within 10 days of its isolation from the plant.

Three possibilities then arise. Firstly, the strong similarity between *A. michiganense* and the organism here described may be purely superficial and illusory. Secondly, the two diseases may have been superposed in the case of the striped plants from which the organism was obtained, the method of cultivation adopted by the authors having destroyed the virulence of the parasite so that infection was not obtained. Thirdly, the two organisms are actually identical, the organism being really a saprophyte and growing so strongly in the dead tissue and in artificial culture as to mask the presence of the true parasite. The authors put forward the third suggestion with great hesitation in view of the wide experience of Dr Smith and of the obvious care exhibited in all his work. In this case, however, many of his recorded inoculations seem to have been made by an assistant, and with material derived by crushing diseased tissue. Again, the very viscid nature of the growth of the organism in artificial culture would tend to make one suspicious of the purity of colonies appearing on a plate since such a slime might well conceal a second organism, especially such a one as *Bacillus lathyri*, whose size and shape are so closely similar to those of *Aplanobacter michiganense*. The authors are emboldened to put forward this view by the statement of Smith that "when this organism was first discovered the writer thought he observed motility."

Supposing that *Aplanobacter michiganense* were proved to be a saprophyte the question would arise as to the possible identity of "Stripe Disease" with the "Grand Rapids Disease." On the face of it such a possibility seems to be a remote one. In Smith's account of his disease no mention is made of any external markings either on the stem or the fruit. These are such a very distinct feature of "Stripe" that they could not possibly have been overlooked. The morbid anatomy in the two cases is however identical; the photograph which appears in Smith's work (8), Fig. 72, p. 163, might well have been taken from a section of a "striped" plant. The lesions in the pith and the presence of bacteria which appear in the outer layers of the cortex are quite characteristic of "Stripe" disease.

Moreover, artificial inoculations of plants with *Bacillus lathyri* made in October, when the plants were well developed, have resulted in no more sign of disease than such lesions in the pith as are shown in this photograph. It is only when plants are growing rapidly that the typical stripes are produced upon the stems.

In view of the present work therefore it seems highly desirable that a further investigation of the Grand Rapids Disease should be carried out.

SUMMARY.

(1) A Stripe disease of tomatoes growing under glass is described.

(2) The causal organism is a small yellow bacillus believed to be identical with *Bacillus lathyri*, Manns and Taubenhaus.

(3) The effect of manurial treatment on the incidence of the disease shows that excess of nitrogen increases susceptibility in the plant and this can be largely counteracted by increase of potash.

(4) Different varieties of tomatoes show varying degrees of susceptibility to the disease.

(5) It is tentatively suggested that the Grand Rapids Tomato Disease, described by Smith, may be identical with this Stripe disease and that the organism which has been described as the cause of the Grand Rapids Disease may prove to be a saprophyte.

REFERENCES.

(1) Bailey, L. H. Winter Blight in "Some troubles of winter tomatoes." *Cornell Univ. Agri. Sta. Bul.* 43, p. 149, 1892.

(2) Howitt, J. E. and Stone, R. E. "A troublesome disease of winter tomatoes." *Phytopathology*, vi, p. 163, 1916.

(3) Manns, T. F. "Some New Bacterial Diseases of Legumes." *Delaware College Agr. Exp. Sta. Bul.* 108, 1915.

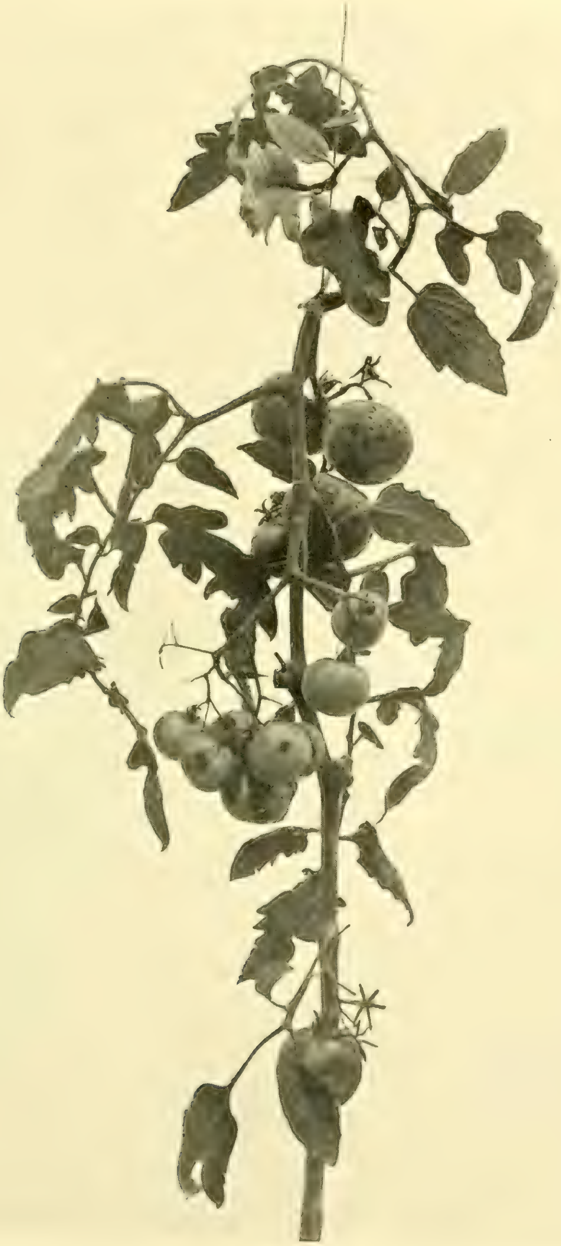
(4) —— and Taubenhaus, J. J. "Streak: A Bacterial Disease of the Sweet Pea and Clovers." *Gard. Chron.* 53, p. 215, 1915.

(5) Paine, S. G. "Internal Rust Spot Disease of the Potato Tuber." *Annals of Applied Biol.* v, p. 77, 1918.

(6) —— and Stansfield, H. "A bacterial Leaf-spot Disease of *Protea cynaroides*, exhibiting a Host Reaction of possibly bacteriolytic nature." *Annals of Applied Biol.* vi, p. 27, 1919.

(7) Selby, A. D. "A Blight of Forced Tomatoes." *Ohio Agri. Exp. Sta. Bul.* 73, p. 237, 1896.

(8) Smith, E. F. "The Grand Rapids Tomato Disease Bacteria in Relation to Plant Diseases." *Washington, D.C.* vol. iii, p. 161, 1914.



A tomato plant badly attacked with Stripe Disease.

NOTES ON THE LIFE-HISTORY OF *EPHESTIA KUHNIELLA.*

By RAYMOND V. WADSWORTH.

Very little has been recorded of the life-history of this moth, although it is so well known and of such economic importance. The writer having had for some years experience of the moth as a warehouse pest, and in breeding experiments, thought that the following record would be of value.

The moth flies during any time of the day or night. Its flight seems to be particularly aimless, as it is not drawn to any of the common devices used to attract insects. Although it has been stated in the *Gordian* that it is attracted by light, the writer has not been able to obtain the least success by this method, and it seems likely that some other small moth was mistaken for *E. kuhniella.* During its life the moth needs no food of any kind, and very seldom if ever takes any, which probably explains the failure of many of the methods of insect capture. It is slow and heavy in its flight, though it can sustain its flight for a considerable time. Above all things, it loves a very still atmosphere. In secluded corners and small recesses where the air is hardly moving, and the atmosphere heavy, the moth abounds and enjoys it to the full, whilst in draughty places scarcely one can be found. Generally it finds its way out of the open into some secluded spot. Cupboards and boxes provide a paradise for it. This dislike of moving air has been hinted at by J. H. Durrant, of the British Museum, in his report on the Army Biscuit question, but not sufficiently emphasised.

The moth lives about a month, laying its eggs towards the latter half of its existence. The eggs are white, 0·0197 in. by 0·0145 in., easily visible to the naked eye, and under the microscope very prettily wrinkled. In laying the eggs the moth does not necessarily display any great maternal feeling, for it will often lay them at a considerable distance from food. Generally however they are placed on the food stuff, singly and not in groups. When the food is in sacks, there are generally holes through which the moth can lay its eggs, but failing this it will lay them on the sacking. The eggs are laid in the darkest corners, as far from the light as possible, and where the material chosen provides cracks and crevices they are placed in these. Thus they are well protected from crushing and from being seen. Never does the moth lay its eggs exposed to the strong light of day.

The larva hatches in a week or so, according to the temperature. If already on food it commences feeding almost at once. If however it is not, or if the food on which it hatches is too hard for its young jaws, it wanders off in search of something sufficiently tender for its delicate age. The outside shell of a cocoa bean, for instance, is too hard for the newly-hatched larva, which will search for a broken shell if born on a bean whose testa is perfect.

Having found its food, the larva with no further ado commences to feed, and eating straight ahead bores its way into the food, leaving only a small hole as evidence of its presence. After a few days it spins itself a silken tube, in which it lives and from which it feeds, and which, if food in its immediate neighbourhood is plentiful, it seldom leaves before it is full-fed. In flour, and such-like fine material, these silk tubes are generally pretty near the surface, but with beans and similar material the tubes are inside the bean, and well inside the bag. At this period of its history, the effect of the larva is not at all evident. The larva is very stationary in its habits, and so the food, especially if it be in bags, appears hardly touched. No larvae are seen, and the silken webbing, so characteristic, is not present. This webbing, so noticeable in most warehouses, is made practically wholly by the full-fed larva in search of a place in which to pupate. The larva loves still air, like the moth, and above all things, darkness. If exposed to the light, it will stop feeding and search for a dark place.

The food of the larva presents interesting variations and influences, as much as the temperature, its length of life. Known as the "Mediterranean Flour Moth," one is apt to think of it as only a flour pest, whereas, as a matter of fact, it is much more widely distributed. It will attack all starchy foods, such as grains of all kinds, dried vegetables, cocoa beans and nuts, and will also feed on jelly cubes and chocolate. The writer has found no instance of its attacking any animal food stored in warehouses, but one peculiarity of its diet suggests that this might be possible. Whenever the larva comes in contact with a dead moth, it accepts the discovery as a delicacy in its diet, no matter what other food is at hand,

and proceeds to make a meal of it. In one instance, the writer kept larvae fed only on Ephestia and Tortrix, for some six weeks. They accepted the diet and outgrew other larvae hatched at the same time and fed on dried beetroot—a favourite food. It thus seems that the larva is fairly broad in its food list, and is unfortunately no epicure. This of course increases the seriousness of the pest, and makes its extermination more difficult. The larva will change its diet fairly readily; from a hard food to a soft food it will change with ease and rapidly settle down, but *vice versa*, though ultimately it will become accustomed to its new food, it will wander far in search of something more to its liking.

The length of life of the larva is generally accepted as being about ten to twelve weeks, but very varying lengths have been given by different authorities. Sharp gives ten weeks or even less, whilst Durrant gives as long as eighteen weeks. The difference arises from the effect of food and temperature. Sharp says, "The enormous increase being due in all probability to the fact that the favourable conditions and equable temperature in the mills promote a rapid succession of generations." It would be well to add favourable food to the above conditions. Under these circumstances there can be as many as six generations in the year, but under more natural conditions the number of generations can be reduced to one per annum. Even however given constant conditions of food and temperature, some larvae will grow very much more quickly than others. Often, larvae will in six weeks reach twice the size of others hatched at the same time. This happens more obviously under poor conditions than under good ones, and of course means the necessary overlapping of generations. The writer has found that very hard foods, such as dried potatoes, will abnormally prolong the life cycle, so that not even one generation is produced in a year. In ordinary circumstances dried potatoes are practically never attacked, even though presenting ideal conditions.

When the larva is full fed, it leaves its silken case and the food on which it has been feeding and goes in search of a safe place in which to pupate. Very seldom indeed does it pupate where it feeds. It is at this stage that the presence of the larva is very noticeable. The bags and walls become covered with silken threads, and numbers of fat and well-grown larvae are to be seen wandering over floors and walls and bags. This exodus in a cool store takes place in August and September, but in hot stores takes place more or less all the time. After some days' wandering the larva has found its place and spins its cocoon inside which it lies with its ventral surface uppermost. Perhaps the favourite spot for *E. kuhniella* is the ears of sacks, where the cocoons can be found crowded together in great numbers, looking almost like one large cocoon; but any suitable crevice will do. If it is autumn, the larva may remain as it is inside the cocoon until next spring, or it may pupate and hatch out almost at once, taking about a fortnight to do so. In the latter case, the insect pairs and lays its eggs at once. These generally hatch, and the winter is passed in the larval form.

NOTES.

By J. C. F. FRYER.

(Entomologist to the Board of Agriculture.)

1. *Charaeas graminis*, L.

Statements as to the stage in which this well-known pest passes the winter are conflicting. Most continental writers suggest that the eggs hatch within a month of the time they are laid (August—September) and that the species hibernates as a young larva. English entomologists, on the other hand, with the exception of Miss Ormerod, state that hibernation takes place in the egg stage. Under the circumstances the following observations may be of interest. A female *C. graminis* captured at Richmond (Surrey) in September, 1918, laid about sixty eggs which were divided into two batches. One batch was placed on a small piece of flower-pot and except for the protection afforded by a cover of perforated zinc was fully exposed to the weather. The other batch was kept in a dry, unheated shed in a glass jar. The latter batch received no moisture while the former was constantly soaked by rain. Although the conditions were different in the case of the two batches, hatching began on the same day—April 7th, 1919, and the great majority of the larvae left the egg within the two succeeding days. No larvae were hatched in the autumn. It would therefore seem that *C. graminis* passes the winter in the egg stage, a point which has a definite economic bearing. Imms and Cole (*Journ. Board of Agriculture*, XXIV, No. 5) suggest that the recent outbreaks of Antler Moth in Derbyshire and other districts are to a considerable extent due to the cessation during the war of the custom of burning hill pastures during March and April. The fact that the eggs of *C. graminis* hatch in April supports this view, for while hibernating larvae buried in tufts of grass or hidden under stones might probably escape the effects of a superficial burning, the eggs or newly hatched larvae would be much more likely to succumb.

2. *Sitotroga cerealella*, Oliv.

This small moth, often known as the "Angoumois Grain Moth," is regularly imported into Great Britain by means of infested cargoes of grain—notably of maize—from America where it has proved a serious pest. In the warmer countries of the world it breeds in the open, in the grain fields, but in temperate regions its increase is confined to warehouses, etc., in which the temperature remains fairly high. It was therefore a surprise when, in October, 1918, two specimens of the moth emerged from some ears of barley grown on a small experimental plot near Kew. The pupae from which the moths had emerged were discovered in the ears and from the circumstances under which the latter were obtained there is no doubt but that the eggs must have been laid on the standing crop in the field. The probable explanation is that moths had emerged from infested grain on one of the barges passing up the Thames and by chance had discovered the barley. There is little likelihood of the species becoming a field pest in the British Isles but its breeding in the open is perhaps worth putting on record.

3. *Anthonomus pomorum*, L.

There seems to be a need for further observations on the habits of the adult beetles of this species during the time which elapses between their emergence from the pupae and their entry into hibernation. Among other points the extent to which the insects feed seems to have been disputed and it may therefore be of interest to record that in captivity a number of the weevils fed actively on apple foliage, attacking the undersides of the leaves but leaving the upper cuticle and the veins. On the other hand beetles kept without food all died. While dealing with *Anthonomus* it may also be worth recording that the beetles on which the above notes were made were obtained as larvae and pupae from an orchard in Hereford which was very seriously attacked. No accurate attempt was made to record the percentage of weevils killed by the parasite *Pimpla pomorum* Ratz., but it was certainly less than 1 per cent. in marked contrast to figures obtained from a Cambridgeshire sample recorded by Imms in a previous number of this Journal (vol. IV, p. 211).

4. *Phyllobius urticae*, De G., and *P. oblongus*, L.

For several years about thirty acres of strawberries on a large fruit plantation in Hereford have suffered very seriously from the attacks of weevil larvae at the roots, the damage in one year being estimated at £1000. Examples of the larvae were examined in March, 1919, and although they exhibited minor differences which appeared to separate them from *Otiorrhynchus sulcatus*, F. and *O. picipes*, F. they were nevertheless attributed to that genus. On May 15th, however, adults began to appear in the breeding cages and in all cases proved to be members of the genus *Phyllobius*, *P. urticae* being the predominant species with a few *P. oblongus* in addition. About the same date the owner of the plantation wrote to say that he also had been breeding out adult winged weevils but in his case all appeared to be *P. oblongus*. Unfortunately no examination of the plantation was made until June 6th, when *P. oblongus* was still present in large numbers but *P. urticae* appeared to have gone, none being found even in the adjacent hedgerows. The plantation had been sprayed very heavily with lead arsenate and it was said that vast numbers of *P. oblongus* had been killed.

At this time curiously enough there were still a few larvae indistinguishable from those of *Phyllobius* at the roots of the strawberries, but none have been reared and their identity is therefore unknown.

Larvae of the genus *Phyllobius* do not in the past seem to have been regarded as of much economic importance either in Britain or on the continent. Reh (in Sorauer's *Handbuch der Pflanzekrankheiten*, III, p. 544) says that they are not harmful with the exception of those of *P. glaucus*, Scop. (*P. calcaratus*, F.) which he records on the authority of Ritzema Bos as having caused damage to the roots of strawberries. However, this note is written without any extensive reference to the literature on the genus and it is possible that there is more information available.

REVIEW.

Miyake, T. "Studies on the Fruit-flies of Japan. I. Japanese Orange Fly." *Bull. Imp. Agric. Sta. Japan,* Vol. ii, 1919, pp. 85–165, Plates II–X.

This excellent and well illustrated monograph deals with the Japanese fruit-fly, *Dacus tsueonis* sp. nov. The insect is described in detail, and the author also gives a good description of the external structure and an account of the alimentary and reproductive systems. The larva is discussed very fully and a good deal of information is given of its internal and external anatomy. In the bionomics of the fly some interesting features are brought to light. Thus, the imagines are strongly attracted to citronella oil, like those of several other species of the genus. Raspberry syrup is apparently almost equally attractive, but kerosene has little or no value in this respect.

There appears to be but a single generation in the year, and the species is limited to the island of Kiusiu in its distribution. Its destructiveness usually amounts to from 10 % to 20 % of the orange crop, but when severe it reaches 50 %. The ovipositor pierces the skin of the fruit and reaches the pulp, where the eggs are laid; thick-skinned oranges are for this reason usually exempt from attack. When the larva is fully grown, the infested fruit falls, and pupation takes place in the soil. No certain parasites of this insect have so far been discovered. The author recommends capturing the flies by means of a kind of racquet smeared with bird-lime; infested fruits should be collected as soon as possible, and can be utilised for the preparation of citric acid. Storehouses should be improved and provided with hard floors, in order to prevent any larvae issuing from infested fruit from entering the earth for purposes of pupation. The paper concludes with descriptions of five new Japanese Trypaneidae.

A. D. I.

VOLUME VI APRIL, 1920 No. 4

ON THE RELATIONS BETWEEN GROWTH AND THE ENVIRONMENTAL CONDITIONS OF TEMPERATURE AND BRIGHT SUNSHINE.

BY WINIFRED E. BRENCHLEY, D.SC.

(*Rothamsted Experimental Station.*)

(With 13 Text-figures.)

IT is fully recognised that the amount of growth made by any crop in the field and the rate at which maturity is reached is influenced by many factors such as temperature, rainfall, season, sunlight, soil conditions and available plant food. There is, however, little definite information as to the influence of each of these factors on a plant at various stages of growth nor with regard to the changes in the actual rate of growth at different periods from the seedling to the mature plant.

It is difficult or even impossible to gain this information from crops growing under normal conditions in the field, because some of the factors cannot even be measured with any degree of accuracy and all are so intimately associated that the action of one or other can hardly be disentangled from the rest. Simplification is therefore essential and some method must be adopted whereby certain of the factors are controlled and kept as constant as possible, thereby reducing the number of the variable influences to be observed. The method of water culture was therefore used, as it enables a strict control to be placed on the food and water supplied, it permits of the roots being observed and weighed with far greater accuracy than in soil experiments, and its compactness allows of a large number of plants to be given individual treatment at the same time. It is also possible to keep a close watch on the temperature variations to which the plants are subjected and to observe the effect of these variations on a number of individuals at different stages of growth.

ENVIRONMENTAL CONDITIONS.

The experiments were carried out in a roof greenhouse specially constructed for water culture work and extended over a period of sixteen months from September 1915 to January 1917. As Rothamsted is situated in a country district away from the fogs that are common to urban areas the light conditions were good for any given period of the year. This is an important point, as Gregory[1], in experiments on cucumbers at Cheshunt, near London, has shown that with high temperatures light becomes a limiting factor, *i.e.* although other conditions are favourable the growth is limited by the deficiency of light. Artificial heating was installed and the minimum temperatures were kept above freezing point throughout the winter months so that the results, so far as they refer to the effect of minimum temperatures, are only applicable in cases where the latter do not fall below 32° F. Throughout the period the maximum and minimum temperatures were recorded daily except on Sundays, but as the thermometers were read at 9 a.m., the Monday readings included those for both the preceding days, thus insuring that a high maximum or low minimum on Sunday was not lost. The weekly numbers of hours of bright sunshine cover the seven days as they are taken from the daily records made at Rothamsted.

For the whole period of sixteen months the prevailing conditions of temperature and light, as indicated by the weekly means of maximum and minimum temperatures (Fig. 1), and the weekly hours of bright sunshine (Fig. 2), are summarised in the following table:

		Mean	Standard deviation
C.	Mean maximum temperature	66·5° F.	11·7° F.
D.	Mean minimum temperature	45·9° F.	4·66° F.
E.	Hours of bright sunshine	20·3	16·6

The mean maximum temperature is naturally greatly influenced by the amount of sunshine, thus partly accounting for the large standard deviation. The minimum is much less variable, as during the winter months special care was taken to keep the night temperatures at a reasonably high level by means of artificial heating.

There is a close correlation between these three environmental conditions. The effect of each on the others depends upon the individual characteristics of the house, such as aspect and ventilation and artificial heating, and the extent of these effects can be measured by the correlation, as follows:

$$r_{CD} = + \cdot 6284 \pm \cdot 0384$$
$$r_{CE} = + \cdot 7560 \pm \cdot 0271$$
$$r_{DE} = + \cdot 2895 \pm \cdot 0595$$

---

[1] 1917. *Third Annual Report of Experimental and Research Station, Cheshunt, Herts*, p. 22.

The close association of hours of sunshine with maximum temperature is to be expected; nevertheless, taking into consideration that the mere total of weekly sunshine ignores its distribution between the several days of the week and the hours of its incidence on individual days, the value obtained, ·7560, is remarkably high. The correlation between mean maximum and mean minimum temperatures is also high, as is naturally the case; but the correlation between bright sunshine and mean minimum temperature would be higher, owing to the close association

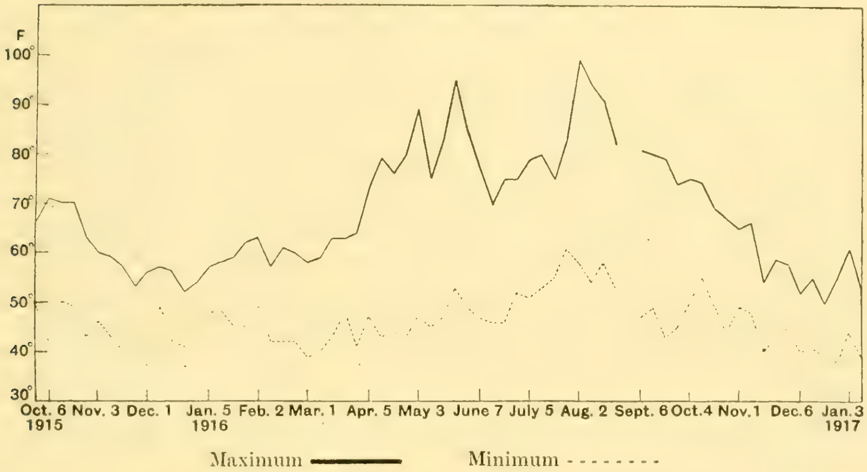


Fig. 1. Average weekly temperatures in roof water-culture house, Sept. 29th, 1915—Jan. 10th, 1917.

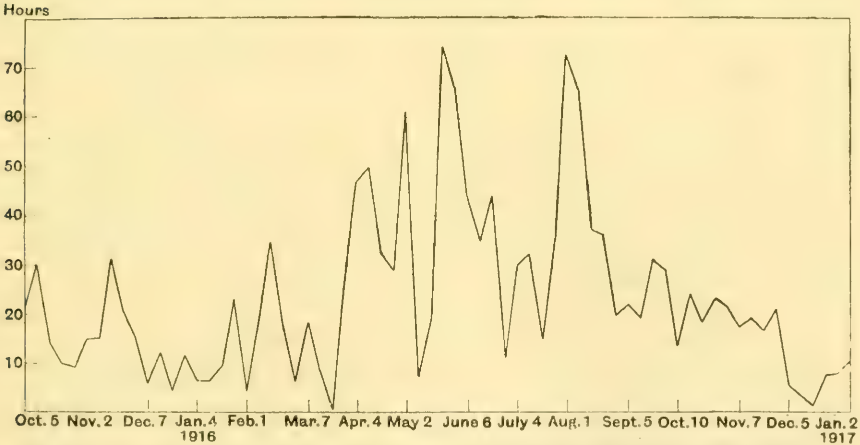


Fig. 2. Total hours of bright sunshine per week, Sept. 28th, 1915—Jan. 9th, 1917.

of both with the mean maximum, if some contrary tendency were not in operation. This is brought out by the partial correlations

$$
\begin{aligned}
{}_{E}r_{CD} &= + \cdot 6534 \\
{}_{D}r_{CE} &= + \cdot 7709 \\
{}_{C}r_{DE} &= - \cdot 3638
\end{aligned}
$$

The correlation between mean maximum and mean minimum for constant sunlight is + ·6534, slightly greater than before, showing that variations in sunlight affect these two variables in opposite directions; the correlation between mean maximum and sunlight for constant mean minimum is also greater, showing that the variations in mean minimum have tended to obscure this high correlation, a high mean minimum tending to occur with high mean maximum but with *low* sunlight. The third partial correlation, that between mean minimum and sunlight for constant mean maximum is strongly negative, and explains how the other two correlations have been obscured. The weeks of high sunshine are evidently the weeks of much radiation and night cooling; this partially counteracts the effect of high day temperatures produced by sunlight.

The small effect of sunshine on the range of mean minimum temperatures is brought out in Fig. 3, which shows that with considerable increase in total sunshine for a specified period (11 weeks) the highest mean minimum temperature is very little raised and the total range of weekly mean minima is little affected, at the same time that the highest mean maximum is pushed up many degrees and its total weekly range is greatly extended. It will be shown later that this relatively constant range of mean minimum temperature over prolonged periods is of great importance to the healthy growth of plants under these conditions of life, and that a comparatively slight increase above a certain level is very detrimental, but fortunately does not often occur.

METHOD.

It was necessary to select a species of plant for experiment that would grow under water culture conditions throughout the year and would not show too great a variation in the growth of individuals of the same age from a single sowing. Several years experience had shown that barley and peas are among the most satisfactory subjects for treatment by this method. In many respects barley is the better of the two, as if a pure line is used and the seeds are graded, very even growth can be obtained. Unfortunately during the winter months, in the "dead" season of the year, it is often impossible to get satisfactory germination of barley, as root development is usually inhibited, and even if seedlings are obtained the young plants make very little growth. Consequently

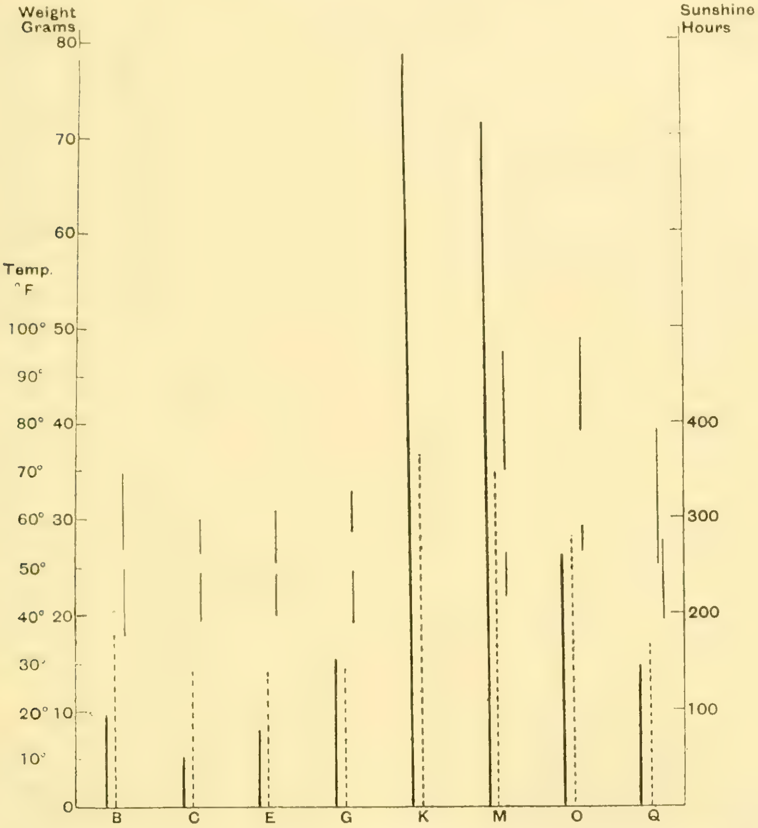


Fig. 3. Graph showing relations between total growth, total hours of sunshine and the range of mean maximum and minimum temperatures for several series of pea plants grown in water culture at different times of the year. All series were grown for 11 weeks except O, in which the plants died prematurely at the end of seven weeks.

Nutrient solutions changed weekly.

Heavy line = total growth.
Dotted line = total hours of sunshine.
Upper light line = range of maximum temperatures.
Lower light line = range of minimum temperatures.

peas were selected, for although the individuality of the plants is rather more marked, seedlings can be obtained throughout the winter, and a certain amount of growth can be relied on at whatever time the experiments are started. A dwarf variety, "Sutton's Harbinger," were used for the majority of the tests, but as unfortunately the stock ran out and could not be replaced the last four tests had to be carried out with Sutton's "King of the Dwarfs[1]."

The seeds were graded and ranged between ·25–·3 gms. or ·3–·35 gms. for "Harbinger," and ·3–·35 gms. or ·35–·4 gms. for "King of the Dwarfs," only one range of weights being used in each test. At intervals of a few weeks sets of 160 pea seedlings were put into water cultures. Usually two parallel tests were carried out, in one of which the nutrient solution[2] was changed weekly and in the other the original solution was retained throughout the experiment. The same day that the water cultures were set up ten extra seedlings were prepared for drying, in order to obtain the initial dry weight of the plants. In addition 10 seeds of the grade used were weighed, to give the relation between seed and seedling after germination. At regular weekly intervals 10 plants from each set were removed from their solutions and the roots carefully washed two or three times in clean water to remove adherent food salts. The roots and shoots were separated before drying, and when the plants were in the fruiting stage the pods were removed, and dried and weighed separately. The 10 plants taken each week were selected at random from the whole group, and may be considered to represent more or less accurately the average growth of any similar number of plants at the time. The figures thus obtained were graphed, and the data yield valuable information as to the rate of growth of the pea plant and its relation to certain environmental conditions.

A. NUTRIENT SOLUTIONS CHANGED WEEKLY

The constant change of the nutrient solution ensured that a plentiful supply of food was always available and that starvation effects did not manifest themselves. The supply of water was maintained by replacing that which was lost from the bottles by transpiration from the leaves, and as the tests were carried out in the greenhouse the plants were not

---

[1] Our thanks are due to Mr Martin Sutton for the gift of all the seeds used throughout these experiments.

[2] Nutrient solution:

Potassium nitrate	1	gm.
Magnesium sulphate	·5	,,
Calcium sulphate	·5	,,
Sodium chloride	·5	,,
Potassium di-hydrogen phosphate	·5	,,
Ferric chloride	·04	,,

Distilled water to make up 1 litre.

subjected to rain or wind. Under these conditions the chief variable factors influencing growth were probably

(1) temperature (maximum and minimum),
(2) bright sunshine and light intensity,
(3) humidity of the air.

Of these factors temperature records are available throughout. The sunshine figures give a very incomplete idea of the amount of available light or of the intensity of light but unfortunately no apparatus for automatically recording the changes in actual light intensity was available, and this part of the investigation is therefore incomplete. The humidity was not measured as at the time the possible significance of change in this respect was not realised, but readings taken during 1919 show that the range of humidity within the house is considerable. The results of the investigation are therefore chiefly of use in indicating the relationship of temperature and sunshine to the rate of growth at different periods of the life of the plant.

Eight series of peas were grown during these observations, the seedlings being placed in water cultures on the following dates:

"*Harbinger.*"

Series B.	September 28th, 1915.	Series G.	January 4th, 1916.
C.	October 28th, 1915.	K.	March 10th, 1916.
E.	December 2nd, 1915.	M.	April 26th, 1916.

"*King of the Dwarfs.*"

O.	July 3rd, 1916.	Q.	October 3rd, 1916.

When seeds are germinated a loss in dry weight occurs owing to the fact that respiration goes on steadily from the beginning of growth, with a consequent loss of material by oxidation that at this stage is not balanced by the manufacture of fresh plant material. After the seedlings are set up in water culture this loss continues, for the same reason, over a period which varies in length according to the time of year (Figs. 4 and 5). Assimilation, which results in the building up of new substances from the air and the absorbed food salts cannot begin till the green leaves have appeared, and even then some little time elapses before the gain from assimilation balances the loss from respiration. Furthermore, the weights obtained show that the gain is at first very slow, as the leaf surface is initially small, and it is often several weeks before the young plant is again as heavy as the seedling was when first put into the culture solution. For the sake of convenience growth is divided into two periods which will be considered separately.

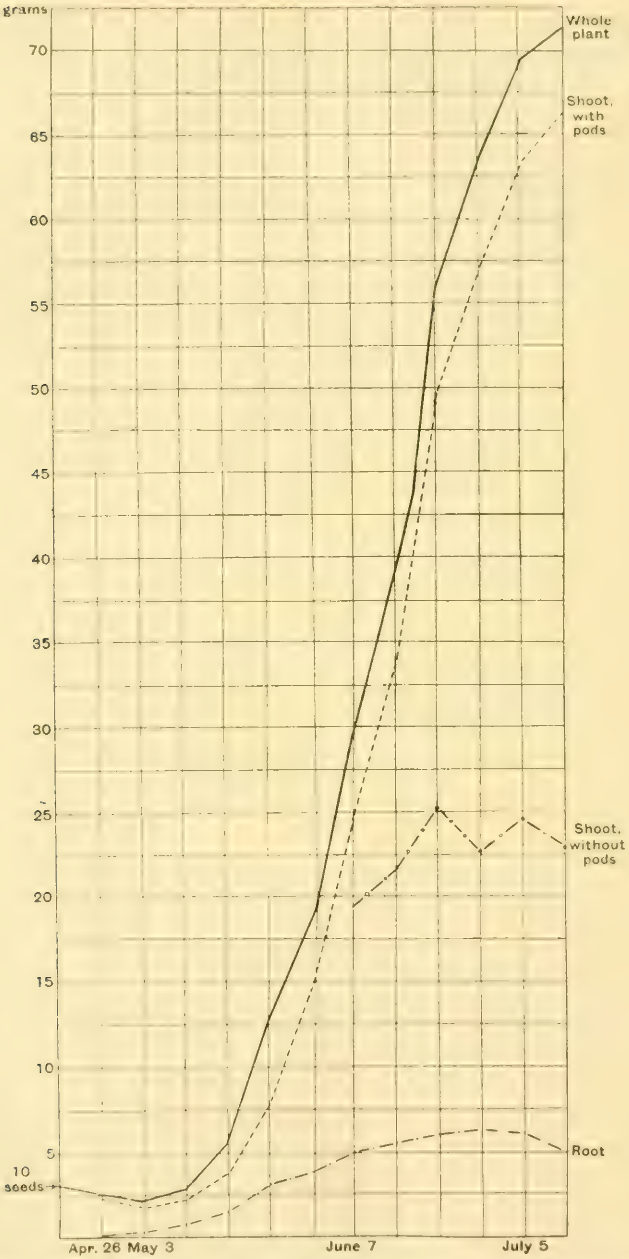


Fig. 4. *Summer Growth.* Dry weights of 10 pea plants, series M, grown from April 26th—July 12th, 1916. Nutrient solutions changed weekly.

(1) *1st period* from the seedling stage till the time that the plant regains its initial weight after the loss by respiration—*i.e.* the time during which a casual observer would say that the plant "makes no growth."

(2) *2nd period*, succeeding the former, during most of which the plant is obviously making growth, and which continues to the end of the experiment.

1st period of growth.

In the division of the plant into root and shoot the remains of the seed are associated with the shoot. From the very first the root increases steadily, though slowly, in weight even while the total weight of the plant is diminishing. This increased root substance is therefore obtained at first at the expense of the shoot and must consist of material transferred from the seed or of the earlier products of assimilation or possibly of both. As the root thus increases in weight all the time, the loss of weight in the whole plant is less marked than in the shoot alone, and it therefore happens that the whole plant regains the initial seedling weight earlier than the shoot does. The length of time taken by the shoot to pass through the first period of growth varied with the time of year according to the prevailing temperatures as follows:

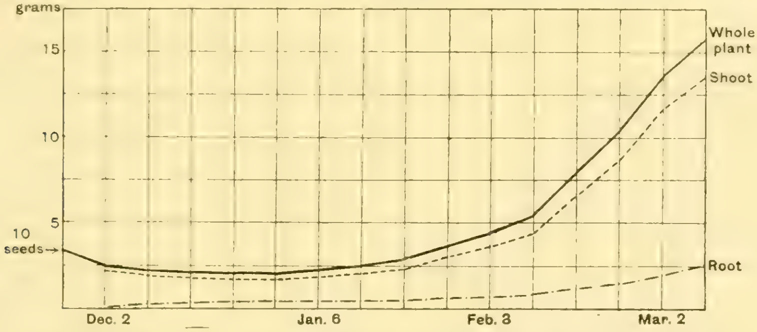


Fig. 5. *Winter Growth.* Dry weights of 10 pea plants, series E, grown from Dec. 2nd, 1915—March 9th, 1916. Nutrient solutions changed weekly.

	Experiment started:	Length of first period for shoot	Max. weekly temp. ° F.	Min. weekly temp. ° F.
B.	Sept. 28th, 1915	3 weeks	70, 69, 70	42, 50, 49
C.	Oct. 28th, 1915	6 ,,	59, 60, 56, 54, 56, 58	46, 43, 40, 41, 37, 49
E.	Dec. 2nd, 1915	7 ,,	58, 55, 53, 56, 58, 59, 59	49, 42, 41, 46, 48, 48, 45
G.	Jan. 4th, 1916	4 ,,	58, 58, 62, 64	48, 45, 45, 49
K.	March 10th, 1916	3 ,,	64, 62, 66	43, 48, 41
M.	April 26th, 1916	2 ,,	89, 75	47, 45
O.	July 3rd, 1916	1 ,,	81	53
Q.	Oct. 3rd, 1916	2 ,,	74, 70	55, 49

If these figures are appropriately grouped it is seen that the length of the first period bears a direct relationship to the range of the mean weekly maximum temperatures; the time decreasing with the rise of the mean maxima. On the other hand the range of the mean minimum temperature seems of little significance as the variations are very irregular and do not run parallel with the length of the first period of growth.

Length of period Weeks	Series	Range of Mean Max. temp.	Range of Mean Min. temp.
1	O	81 ° F.	53 ° F.
2	M	75–89	45–47
	Q	70–74	49–55
3	B	69–70	42–50
	K	62–66	41–48
4	G	58–64	45–49
6	C	54–60	37–49
7	E	53–59	41–49

It is thus evident that the rate at which assimilation is able to make good the loss by respiration increases directly with rise of temperature; at the lower temperatures a very small increase will reduce the period by a week or more, but higher up the scale a slowing off in the time reduction is noticed. It is probable that this is really a temperature effect rather than one due to light intensity, for with similar temperatures the same length of 1st period growth occurred at different times in the year, *e.g.* in series M started on April 26th the period of two weeks was the same as in series Q started on October 3rd, though the light intensity in the first case would probably be greater than in the second, while 68·2 hours of bright sunshine were recorded in the April period and only 42·1 hours in the October period.

The initial stage of growth, therefore, is represented by a period during which the weight lost by respiration is made up by a gain due to the beginning of assimilation, the rate at which this compensation occurs depending on the maximum temperature.

2nd period of growth.

All the series behaved in a similar way during the first period except with regard to the length of time that this persisted. The second period, that of active growth, is very different, and each series presents its own individual characteristics. Analysis of the results obtained, however, show that these characteristics bear a clear relation to the variable factors at work, and that the plant responds definitely and not arbitrarily to change in the environmental conditions.

(a) *Relation of total growth to sunshine and temperature.*

Under ordinary field conditions of cultivation the amount of water supplied as rain and the action of wind in drying out the soil and causing rapid alterations of temperature would influence the direct effect of temperature and sunlight. Under greenhouse conditions the first two factors are eliminated and the enquiry can therefore be narrowed down. In order to work out the relationship of total growth to sunshine and temperature it is essential that the growth should have occurred over equal periods, and for this reason only the first eleven weeks of each series are considered. One series, O, died after seven weeks, and this will be specially considered later on. The results are most clearly demonstrated by Fig. 3, in which are graphed for each series the total growth of the plant, the total number of hours of sunshine over the 11 week period, and the ranges of the mean weekly maximum and minimum temperatures over the same period. As would naturally be expected the total growth in summer was much in advance of that in winter. The three series C, E, G, started in October, December and January, show a steady increase in the total growth, G being more than twice as heavy as C. The available sunshine in all three cases was the same, but the range of maximum temperature was successively rather higher, though the greatest difference was only six degrees (60°–66° F.). In the dead season of the year, therefore, slight differences in maximum temperature are very important in determining the amount of growth and they act independently of the available sunshine. The ranges of minimum temperatures were similar in all three cases and therefore did not influence the result.

The optimum time for growth under the experimental conditions was spring and early summer. In the presence of an abundant and unstinted food supply series K, started in March, made five times as much growth as G, started two months earlier. Double the amount of sunshine was available and the temperature ran up steadily from a rather low level until it almost reached the maximum weekly mean attained during the season. The series M, started a month later, did not do quite as well, but this may have been due to the fact that though the highest mean temperature was the same as K the means for the last three weeks were comparatively low.

A striking point emerged when an attempt was made to grow a series O at the beginning of July. The weather was bright and sunny throughout, the seedlings were started at 80° F., for only one week did the mean temperature fall as low as 75°, and for three weeks the average maximum was above 90° F. The plants were unable to stand the strain and after seven weeks growth they were dead, having made only 28 gms. dry matter compared with 39 gms. produced during a similar period in series M more than two months earlier. The mean minimum temperatures were comparatively high, the lowest mean being equal to the highest recorded at any other period. Evidently constant high temperature combined with excessive insolation under glass are inhibitory to growth, the best results being obtained with rather less sunshine and a greater range of temperature.

Autumn plants started in September and October resembled those grown in the winter, with a certain amount of extra growth due to a rather more generous supply of sun and heat.

It is thus seen that the possible amount of growth depends directly upon the sunshine and temperature at all periods of the year, but that beyond a certain point these beneficial factors become harmful and result in the premature death of the plants. Usually the two factors work together but when one factor, sunshine, remains constant, temperature is able to act independently in influencing growth. The converse of this may also be true but has not been demonstrated in these experiments.

(*b*) *Relation of the efficiency index to the time of year and the age of the plant.*

The "efficiency index" represents the rate per cent. at which fresh material is continuously added to the plant over a definite period[1], and it provides a very useful means of indicating the rate of growth at different periods of the life of a plant. In Fig. 6 the efficiency indices are plotted for weekly periods for all the series. As has already been stated during germination the seedlings lose weight by respiration, so that at the very beginning they weigh less than the seeds from which they came, and during the early part of the first growth period a further loss occurs until assimilation is in full play. At these stages the efficiency indices are negative, but when growth has fairly set in they are always positive, except occasionally at the very end after active growth has ceased but respiration is still continuing.

The curve shows at a glance that during the summer months, while growth is rapid, the efficiency indices reach a high level; in the spring and autumn they are medium, whereas in the depth of the winter they are very low and indicate that little more growth is made than will provide material to keep the plant alive and progressing very slowly.

---

[1] Blackman, V. H. (1919). "Compound Interest Law." *Ann. Bot.* XXXIII, pp. 353–360.

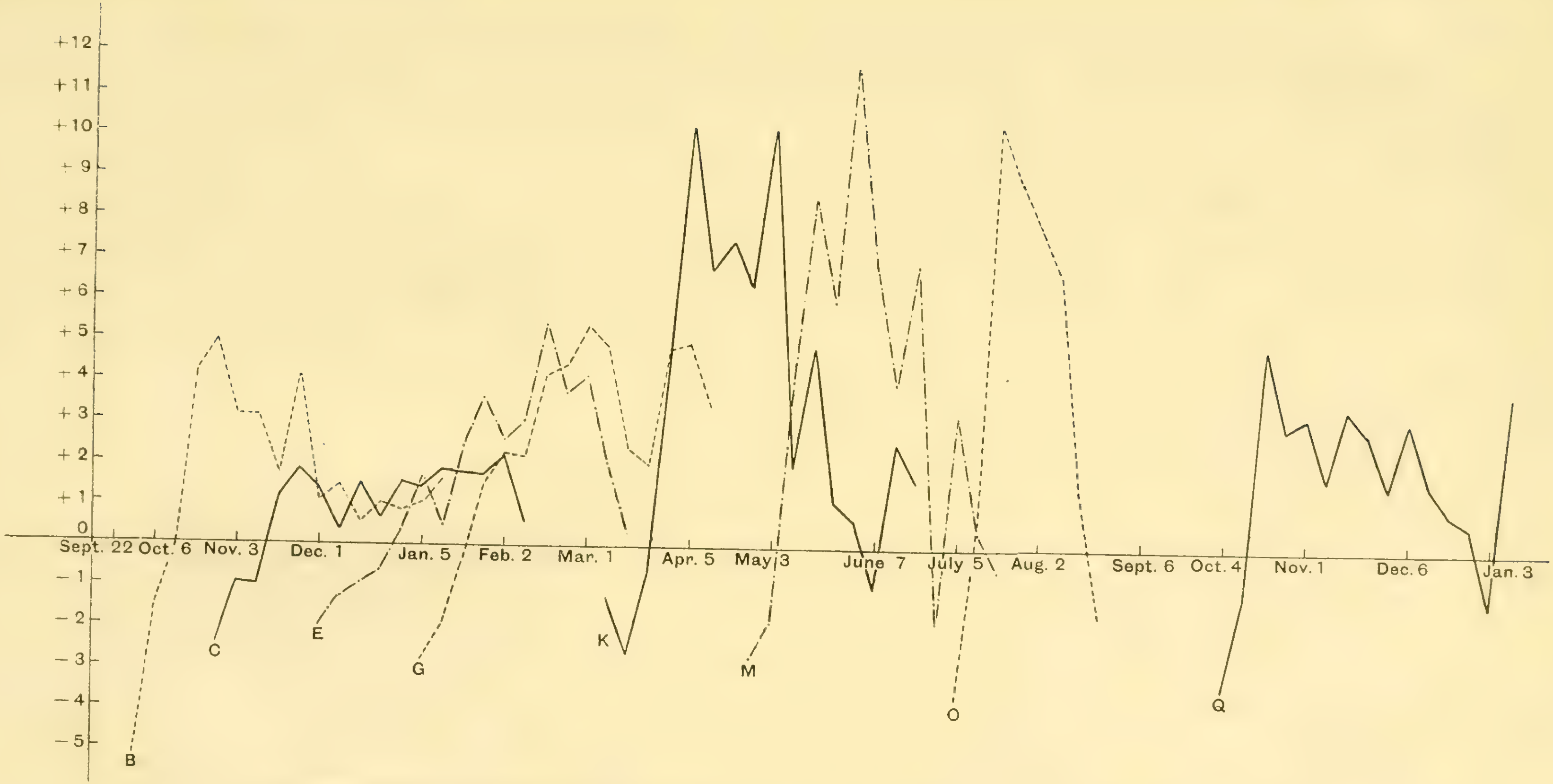


Fig. 6. Mean efficiency indices (per cent. rate of increase) per day over weekly periods. Nutrient solutions changed weekly.

Low efficiency indices were the rule from September to April[1], nearly all being below 5. During this period practically all the maximum temperatures were below 65° F. (see Fig. 1) and although the sunshine curve was much less regular than that of temperature all the weekly sunshine totals were below 35 hours, seven being below 7½ hours (see Fig. 2). During December the efficiency indices were very low and only varied within small limits, being much the same in series of different ages, which is not usually the case. This is evidently connected with the fact that during December occurred the lowest group of maximum temperatures for the whole year, and the period also embraced the largest group of low sunshine records. A rise in the indices began in January coinciding with an improvement in both temperature and sunshine. From March to August[2] high efficiency indices, much over 5, were obtained. Throughout this period the maximum temperatures were above 65° F. except during the first four weeks when they were slightly lower. Fifty per cent. of the weekly sunshine totals exceeded 35 hours, the excess often being considerable, six totals being 50 or more hours, while none ran below 7½ hours as happened earlier in the year. Thus broadly speaking high efficiency indices are associated with high temperatures and plenty of sun, while low indices occur in cold weather with deficient light.

Within this generalisation, however, more detailed information can be worked out.

An examination of the curves (Fig. 6) shows that during the greater part of the year, from March to November, the efficiency indices rise to their maximum very early in the life of the plant, usually within one or two weeks from the close of the first period of growth. In spring and autumn this maximum efficiency index is not very great, in summer it is much larger, but, given a moderate or plentiful supply of heat and sunshine, the impulse of the plant is to attain its maximum rate of growth as early in life as possible. This, of course, tends to the production of larger plants, as rapid growth at the beginning provides a large leaf surface at an early date so that more assimilation and increase of material can take place. When plants are started in the winter, in December or January, this rapid rise to the maximum does not occur, but the efficiency indices slowly climb up, taking about five weeks from the end of the first growth period to attain their maximum. This is associated with low maximum temperatures and low sunshine totals extending over the whole life of the plant, so that at no time is the growth encouraged by a spell of greater heat or more abundant sunshine. As soon as the rate of growth reaches its maximum in the spring and autumn it begins to fall off slowly and irregularly but as at these times of the year growth was not completed within the period of experiment it is not certain what the behaviour would be at the end of growth. In the summer the rate of growth tends to fall away from the maximum but remains very high for several weeks. During this period the plants probably reach their maximum efficiency, making the fullest use of the food supplied under favourable conditions of temperature and sunshine. Growth is so rapid that it draws to a close towards the end of the experimental period and this is indicated by a sudden drop in the efficiency index, which occasionally becomes negative at the very end, indicating the continuance of respiration after assimilation has ceased, possibly combined with some degree of desiccation. The maintenance of a high rate of growth for several weeks during the summer combined with a sudden later drop is in marked contrast to the slow steady fall in the earlier part of the year, and explains fully why the later sown plants are so much more weighty than the rest. The later fall in the indices is not determined by either temperature or sunshine, but is a characteristic feature in the physiology of the plant occurring towards the end of growth, but the degree in which the fall is marked does depend to some extent upon the environmental conditions, as it is more obvious when favourable circumstances have kept up a rapid rate of growth until late in the life of the plant. The importance of the rapid rise to the maximum rate of growth is well shown by series K and M, both grown in the summer months. M reached a considerably higher maximum efficiency index than K, but whereas in K the rate of growth was at its maximum within a week of the 1st period, in M three weeks elapsed before this point was reached. Consequently, in spite of the ultimate rate being higher in M, the total growth was only 71 gms. against 91 gms. in K.

---

[1] First series started in September, last series ended in April.

[2] First series started in March, last series ended in August.

In the July series O the effect of the excessive heat and insolation was not manifest at first, as the maximum rate of growth was reached at the usual time, one week after the end of the first period. The rate fell off steadily though not abnormally quickly for another three weeks, but by that time the energy of the plants was exhausted and during the next fortnight the efficiency index fell rapidly until at the end the plants were prematurely dead.

An examination of the data by statistical methods shows a remarkable agreement with the results deduced by observation during growth and comparisons of the figures and curves for the individual series.

Of the factors which affect the relative rate of increase of growth age, maximum and minimum temperatures and hours of sunshine can be investigated from the available data. The relation between age and rate of increase over the whole life is far from linear, so that the simple formulae of partial correlation cannot be applied, but the series of mean relative rates of increase may be divided into two satisfactorily linear series by separating the young plants (mean age up to four weeks old) from the old plants (mean age over four weeks). During the first period the mean efficiency indices rise to a maximum and during the second they fall from the maximum. This result bears out the observations that growth is divided into two distinct periods and that the tendency is for the maximum rate of growth to be attained at the beginning of the second period and to fall off afterwards.

When allowance is thus made for age the effect of environment upon the young and old plants must be considered separately.

The actual correlations between relative rates of increase (efficiency index) and the four other variates, age and the three environmental measurements, are

	Young plants	Old plants
Age	+·6995±·063	−·3498±·065
Mean maximum temperature	+·4444±·097	+·3907±·063
Mean minimum temperature	+·3958±·104	−·0588±·074
Bright sunshine	−·0132±·123	+·5177±·056

The quantities measure the extent to which the variables concerned are actually associated; growth in young plants is thus associated with relatively warm days and nights but not significantly with sunshine, in the older plants it is associated strongly with sunshine and warm days but not significantly with the night temperatures.

The combined effect of the independent variation of these four quantities may be expressed by regression formulae, the coefficients of which can be calculated from the correlations. If A stand for the age measured from a mean value of 2·5 weeks and 10 weeks for young and old plants respectively, C the mean maximum temperature measured from 67° F., D the mean minimum temperature measured from 46° F. and E the hours of bright sunshine in excess of 21 per week, then the relative rate of increase of young plants has the regression formula

$$\cdot03 + 1\cdot9544A + \cdot3586C - \cdot0190D - \cdot1551E,$$

while for the old plants it is

$$2\cdot91 - \cdot2121A + \cdot07515C - \cdot2320D + \cdot0619E.$$

In interpreting these formulae it should be remembered that as C, D and E are closely associated the alteration of any one of them without the other is to some extent an unnatural process. Thus the fact that in both formulae the coefficient of D is negative, in the first to an insignificant extent but in the second significantly, shows that the greater growth has in general been made with the lower night temperatures *after allowance has been made* for the cooler days and less sunshine which are in fact associated with cooler nights. In the same way sunshine is detrimental to the seedlings *after allowance has been made* for its beneficial effect upon the day temperatures. Once the average effect of the environmental conditions is ascertained it is possible to obtain a truer representation of the relative rate of growth at different ages. For this purpose the average of the relative rates of increase for any age is corrected by means of the regression formula to its probable value under standard environmental conditions. The result of so doing is shown by comparing Figs. 7 and 8. The falling off of growth with age is more gradual after allowance has been made for changing environment; the points lie closer to the regression line for the older series, but the four first series are distinctly less linear. The whole series so corrected is likely to give a much truer picture of the normal history of the plant than when no correction is made. On the other hand, it is clear that irregularities are still present though they are smaller, and the three measures which have been used evidently do not give a complete picture of the plant's environmental experience during the week to which they refer. Among the other factors of environment that cause these irregularities are probably the distribution of the hours of sunshine over the day and week, the variation in the actual intensity of light apart from bright sunshine and the humidity of the surrounding air.

The abrupt rise in the relative rate of increase for the mean 9th period may possibly be mere coincidence but is more likely to have a physiological significance. Examination of the actual curves of efficiency indices show that somewhere in the neighbourhood of this period a real or secondary maximum efficiency index occurs, and in several cases the data show that just at this time the plants were in their first flush of flowering. This rise may therefore be real and connected with the initiation of sexual reproduction. If this be so it affords an interesting parallel to the increase in growth occurring at the time of puberty in human beings[1].

---

[1] Hall, G. S. (1908). *Adolescence*, Vol. I, pp. 59, 84, 93, 99.

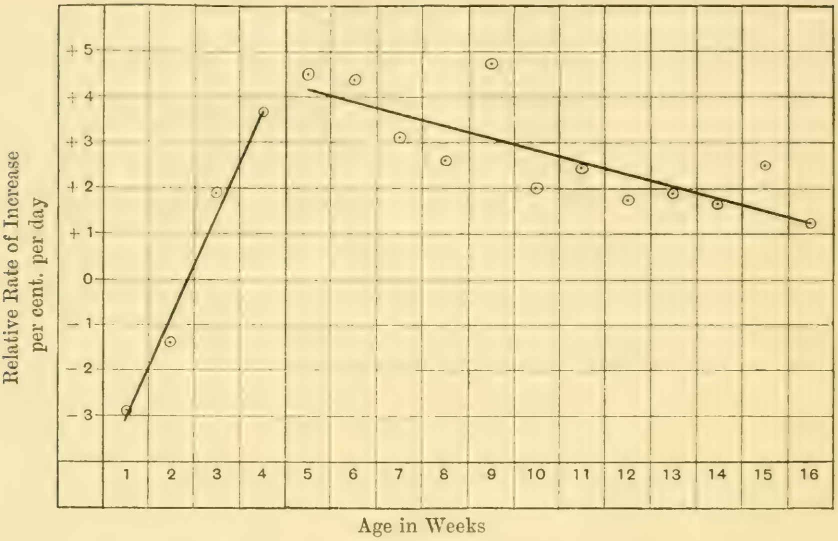


Fig. 7. Mean relative rate of increase at each age, with regression lines for young and old plants.

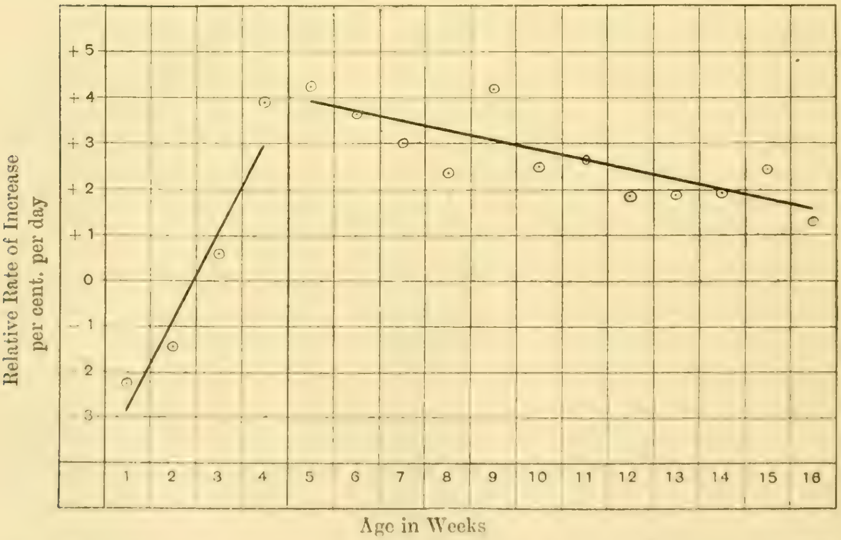


Fig. 8. Mean relative rate of increase at each age reduced to standard conditions, with regression lines for young and old plants.

Mean Maximum Temperature—67° F.
Mean Minimum Temperature—46° F.
Bright Sunshine—21 hours.

B. NUTRIENT SOLUTIONS NEVER CHANGED.

1st period of growth.

The series in which the solutions were never changed were set up to correspond in time as closely as possible with those in which the food was renewed. The following table shows how exactly the two sets correspond with regard to the length of the first period of growth.

Solutions never changed			Solutions changed		
	Series started	Length of first period of growth for shoot Weeks		Series started	Length of first period of growth for shoot Weeks
A	*Sept. 23rd,* 1915	2	B	*Sept. 28th,* 1915	3
D	Oct. 29th	6	C	Oct. 28th	6
F	Dec. 4th	7	E	Dec. 2nd	7
H	Jan. 5th, 1916	4	G	Jan. 4th, 1916	4
I	Feb. 19th	4	No corresponding set		
L	March 10th	3	K	March 10th	3
N	April 26th	2	M	April 26th	2
P	July 3rd	1	O	July 3rd	1
R	Oct. 3rd	2	Q	Oct. 3rd	2

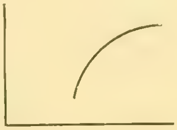
The only instance in which the first period varied by even a week was when there was five days difference in the date of beginning the experiment. At that time of year, in September, both temperature and sunlight were falling and the difference of nearly a week would fully account for the prolongation of the first period of growth in the later started plants. This series is therefore left out of consideration in drawing up comparisons. The close correspondence shows that during the first period of the plant's development under the experimental conditions the presence of an excess of nutrients, below toxic limits, has no effect upon growth. Very little mineral matter is sufficient to supply the needs of the seedling and the fresh quantity given when the solutions are changed is disregarded and exercises neither a beneficial nor harmful action. As a matter of fact, so little food salt is withdrawn from the solution at this time that the fresh solution added weekly closely resembles the old, and it is probable that no difference is detected by the plant.

2nd period of growth.

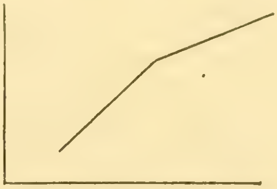
As the series with changed and unchanged food solutions were carried on together the conditions of sunlight and temperature were identical in each case, the only different factor being that in one set an unlimited supply of food was available and in the other a very limited quantity was at the disposal of the plants.

(*a*) *Effect of restricted food supply on total growth.*

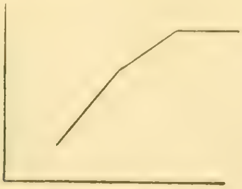
It was to be expected that the unchanged set would make less growth than the others, but the comparative relations of the amount of growth at different periods of the life of the plant are not altogether what were anticipated. As the plant grows and steadily draws on the limited food supply, the available amount of nutrient in the solution correspondingly decreases, and it might have been expected that with this decrease in available food a gradual decrease in growth would occur, giving a curve of the form



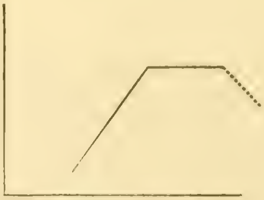
This, however, did not occur in any case. At all seasons of the year the growth in the earlier part of the second period showed a steady rise. In winter when growth was very slow the rise continued throughout the experiment; as the temperature and sunshine increased the time got shorter until eventually the rise reached its maximum in about three weeks. Then, quite abruptly, the growth changed and the curve flattened to a greater or less degree, but when once the change had occurred steady increase was again made, so that in most cases the curve took the form



In the early summer months growth ceased before the end of the experiment, causing a second flattening in the curve, whereas in the height of the summer no further growth was made after the first rise and a later drop often took place on account of loss due to respiration and desiccation.



Early summer.



Height of summer.

It is difficult to suggest an explanation as to why the abrupt changes followed by a period of steady growth should be the rule, instead of a gradual decrease in growth parallel with the gradual decrease in food. A comparison of these series (Figs. 9 and 10), with the corresponding sets with unlimited food supply (Figs. 4 and 5), shows that except during the summer period of very rapid growth the amount of dry matter produced with limited and unlimited food supply is much the same or even identical for several weeks after the end of the first period, showing that the gradual reduction in food material does not always immediately affect growth. Eventually the well-supplied plants continue their steady

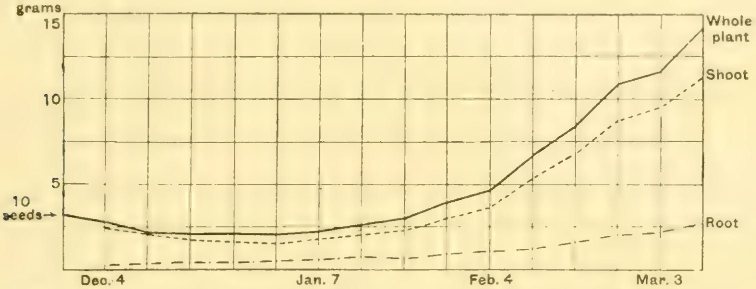


Fig. 9. *Winter Growth.* Dry weights of 10 pea plants, series F, grown from Dec. 4th, 1915—March 10th, 1916. Nutrient solutions never changed.

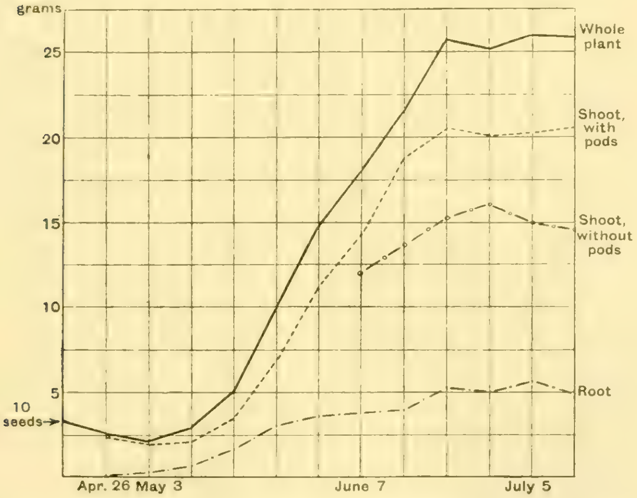


Fig. 10. *Summer Growth.* Dry weight of 10 pea plants, series N, grown from April 26th—July 12th, 1916. Nutrient solutions never changed.

increase but the restricted ones fall off in the manner indicated above. In the summer with optimum conditions the extra food supply is beneficial from the first as the plants have a very high efficiency index and are able to utilise the nutrients to much better advantage, but though the restricted plants cannot keep pace with the others they rise in weight quite steadily for several weeks before depression sets in. It is only in series grown inclusively from March to June that the changed series pull ahead immediately the first period closes, while during the rest of the year the plants either do not begin to take advantage of the full supply in the one case or else they do not feel the lack of the full supply in the other till a later date.

The maximum amount of growth that can be made with a given constant supply of nutrients before growth ceases varies with the time of year, *i.e.* with the environmental conditions. Plants grown during May and June averaged 26 gms. dry matter and the total ranged down to 14 or 15 gms. in plants grown in spring or autumn. The winter grown plants did not reach the stage of ceasing to grow, but judging by the trend of the efficiency index curve it is probable that the dry weight would have been below that of the spring and autumn plants. The reason for this variation in dry matter produced is probably that growth is not only dependent upon the mineral food supplied to the root but also on the quantity of carbohydrates produced by assimilation. Under favourable conditions of temperature and sunlight when assimilation is greatly encouraged the formation of carbohydrate is very rapid and the amount of other constituents of dry matter become proportionately though not actually less. This is illustrated in an exaggerated form by those plants which store up starch or sugar, as potato and beet, but it holds good in other green plants as well. When conditions are less favourable to assimilation less carbohydrate is produced in proportion to the amount of food material absorbed, and with a limited supply of the latter a lower total growth is produced.

One curious discrepancy between the changed and unchanged series is noticeable. The maximum growth with unlimited food supply was made in a series grown from March to May, but in another grown from May to July there was a decided falling off which was attributed to less favourable environmental conditions. With limited food, however, the maximum growth was made in the second set, from May to July, so that apparently the environmental conditions that are optimum for dry weight production in the presence of plenty of food are not necessarily the optimum when a restricted supply is available.

Dry Weight per plant in grams.

	Unlimited food supply	Restricted food supply
March—May	K. 9·2	L. 1·85
May—July	M. 7·2	N. 2·6

(*b*) *Effect of restricted food supply on efficiency indices.*

The general form of the curves (Fig. 11) of the efficiency indices for the various series throughout the year is much the same whether the food supply is abundant or restricted, showing that on the whole there is a similar response to the environmental conditions that are common to both sets. In detail the correspondence is less close, indicating the influence exerted by the variable factor of food. In most cases during the earlier weeks the rates of growth go up or down together in both cases, as at this stage the environmental conditions of temperature and light common to both are more potent than the variation in food supply. Later on, when food begins to be much restricted in the one set, the efficiency index curves no longer run together, and they become much more irregular and erratic in the starved series. Under the conditions of restricted food supply, therefore, changes in the common environmental conditions produce exaggerated effects on the rate of growth. The foregoing applies more particularly to the spring and autumn months, but matters are rather different during the period of most rapid growth in the summer. At this time the conditions of light and heat are so favourable to growth that the plants can take advantage of a very large supply of food, and any restriction in this respect is felt more severely than when growth conditions are less good. Both sets of plants make the most of the available food immediately the first period of growth is over, and rise almost at once to a maximum efficiency index. This greatly depletes the food store, and when no more is supplied the rate of growth cannot be kept up and a rapid fall occurs, in contrast to the prolonged period during which a high rate of growth is maintained in the presence of abundant nutrients. In some cases the restricted plants never attain such a high efficiency index as the unrestricted, and the fall in the rate is less sharp, but in others the maximum index is as high or even higher and then an exceedingly sharp fall occurs, on one occasion (set P) the drop being from 11 to zero in three weeks.

A statistical comparison of the figures relating to the "changed" and "unchanged" series bears out the results obtained from observation of the curves of total growth, but shows more clearly the course of events in the later part of the life of the plant. The mean differences between

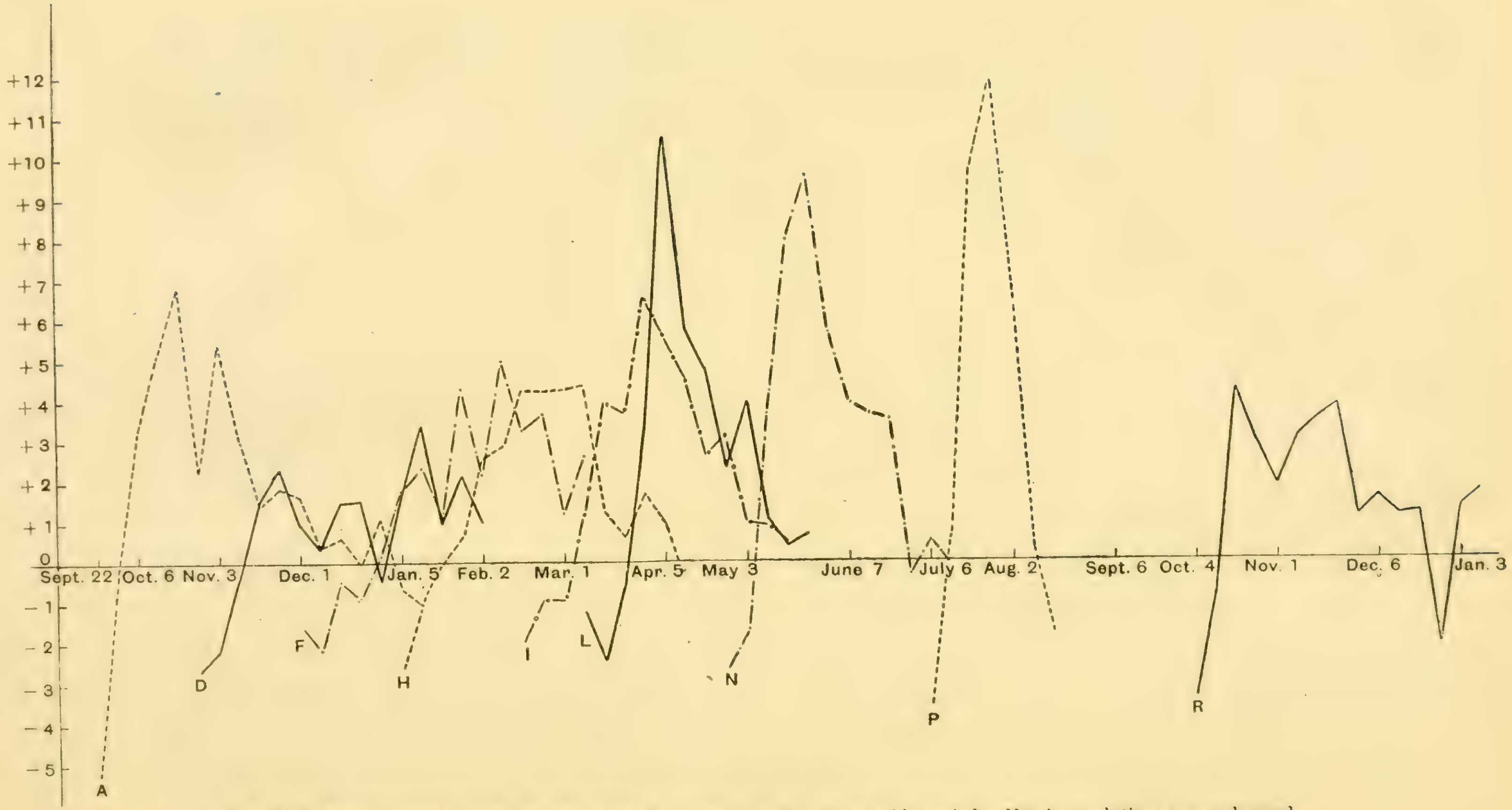


Fig. 11. Mean efficiency indices (per cent. rate of increase) per day over weekly periods. Nutrient solutions never changed.

the relative rates of increase (efficiency indices) week by week are shown in the following table, and are seen to fall into two distinct groups:

Week	Mean difference in efficiency indices of "changed" and "unchanged" series	
1	− ·109 ± ·18	
2	+ ·110	− ·07 ± ·15. Difference insignificant.
3	− ·106	
4	− ·062	
5	− ·220	
6	+ 1·647	+ 1·19 ± ·20. Difference definitely significant.
7	+ 1·119	
8	+ ·993	
9	+ 1·768	
10	+ ·667	
11	+ 1·116	
12	+ ·455	
13	+ 1·700	
14	+ ·997	
15	+ 1·707	

The insignificant differences obtained in the early weeks emphasize the fact that during the first period of growth and for perhaps a short time longer the plant gains no benefit from the constant renewal of the nutrient solutions, probably because during this time the demands on the external sources of nutrition are comparatively small, as some supply is still available in the seed and the manufacture of fresh food by assimilation is not yet in full swing. When once this period is over the variation in food supply makes itself felt at once, and this continues throughout the life-history. No constant change in the difference of the rate of increase is observable, but the variations are irregular throughout. This is somewhat contrary to expectation, as it was surmised that the drop in the efficiency indices in the unchanged series in late life would be far greater than that in the changed sets where no starvation effects were manifest. Apparently the natural fall in the indices that occurs late in life in all cases was more or less parallel to that induced in the semi-starved plants.

The correlations between relative rate of increase (efficiency index) and the three environmental measurements for the "unchanged" series are as follows:

	Young plants	Old plants
Mean maximum temperature ...	+ ·4760	+ ·1695
Mean minimum temperature ...	+ ·4170	− ·0619
Bright sunshine	+ ·0300	+ ·4263

When these figures are compared with those for the "changed" series given on page 226, it is seen that with the young plants little difference occurs, showing that in early life the amount of food supplied in both sets was in excess of requirements and did not therefore act as a limiting factor. With older plants, however, when the food solutions were not renewed the correlation of rate of increase with mean maximum temperature was very much lowered and that with bright sunshine was also reduced to a significant extent. This indicates that when scarcity of food is acting as a limiting factor the plants are unable to take full advantage of the available bright sunshine, while at the same time the beneficial influence of high maximum temperature is reduced to an even greater degree.

Another interesting point can be elucidated from the comparison of seven pairs of changed and unchanged series, each pair being grown under identical conditions for the same length of time. The total variance[1] at any given age, for older plants (in the second period of growth), may be roughly analysed into

37 per cent. fortuitous variation (due to individual difference of seeds etc.).
38 per cent. known environmental factors.
25 per cent. unknown environmental causes (irregularities of temperature and light not affecting the means, humidity etc.).

The percentage of variance (38 per cent.) that can be attributed to the known environmental causes of maximum and minimum temperatures and total sunshine is remarkably high and indicates that these are the most potent of the factors acting upon growth. The causes of fortuitous variation are less clear, and the percentage (37 per cent.) seems rather high considering that it is a mean figure, as under the greenhouse conditions the extremes of individual variation in a number of plants generally reach about the same figure, and the mean variance in the rate of increase might be expected to be less. The extent of individual variation in weight, however, regarded as a percentage difference, must not be confused with the variance of the efficiency index which is to be ascribed to various groups of causes. Further work on this point will be necessary, for if it could be more fully explained it would give more reliable information than is at present available as to the influence of the individuality of plants upon the validity of experimental results.

---

[1] The mean square deviation of the rate of increase at given age is used as a measure of the variance, and the percentage figures are calculated from this.

GENERAL OBSERVATIONS ON GROWTH.

(1) *Comparison of root and shoot growth.*

Inspection of the growth curves shows that at all stages of growth and at all seasons the dry weight of the root is less than that of the shoot. As the plants get older the shoot becomes rapidly heavier under favourable conditions, but the increase in root weight is by no means parallel to that of the shoot as it is very much slower, with the result that when very heavy growth is ultimately made by any plant the discrepancy in the dry weight of the root and shoot is very marked. This change in the relations between the two parts of the plant is well shown by the ratio between the dry weights of shoot and root for the weekly periods for which figures are available (Figs. 12 and 13).

In the very young seedlings, at the stage at which they are put into the food solutions, only part of the material stored in the seed has been utilised and the roots are as yet very small. Since the seed is included with the shoot the shoot/root ratio at this time is very high, ranging from about 14–32 according to circumstances[1]. From this time more normal relations establish themselves, for the seed store becomes rapidly depleted and the ratio is that between the actual shoot (stem and leaves) and the root. The shoot/root ratio continues to fall at a decreasing rate for a varying period, the lowest ratio corresponding fairly closely with the end of the first period of growth, though it may be reached a week or two earlier or later. From this time onwards, when there is no deficiency of food (Fig. 12), the shoot increases more rapidly than the root in weight, and the shoot/root ratio goes steadily up. The more rapid the growth, the more marked this rise, and in the summer months under optimum conditions of temperature and light the low proportion of root to shoot is most striking. When the food supply is limited (Fig. 13) and less growth is made the figures do not reach such a high level, but exactly the same course of events is noticed, as a rise in the shoot/root ratio occurs from about the end of the first growth period and the largest ratios are obtained in the summer months.

An explanation of this change in the proportion of shoot and root may be found in the different mechanical construction of the two parts. The two main functions of the root are the absorption of water containing dissolved food substances and the fixing of the plant in the substratum. For the efficient performance of the first function a large area capable of constant renewal is desirable in order that the maximum proportion of root hairs, the actual absorbing organs, may be provided and renewed as they die off. The root, with its multiplicity of long slender branches continually growing in length, fulfils this condition admirably and each addition of an extra rootlet provides an additional absorbing surface out of all proportion to the quantity of plant material used up in

---

[1] For economy of space this initial high ratio is omitted from Figs. 12 and 13, the first ratio on the curve being that obtained after one week's growth in nutrient solution.

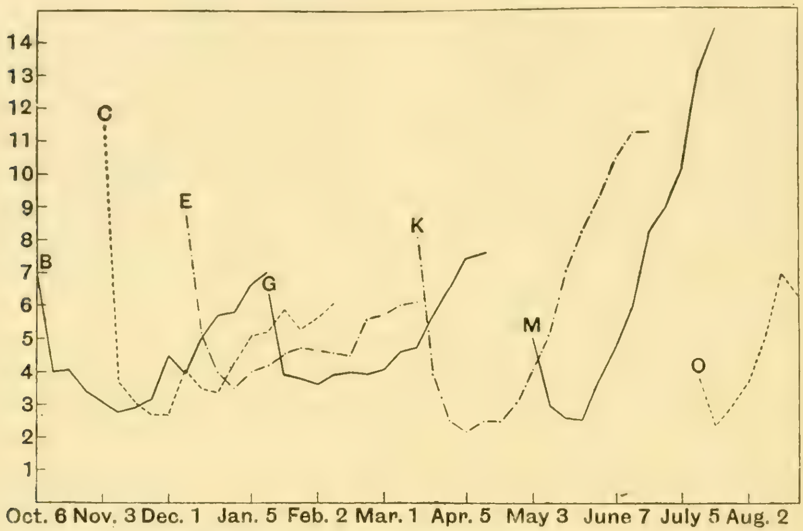


Fig. 12. Shoot/Root Ratios for weekly periods. Oct. 6th, 1915—Aug. 23rd, 1916. Nutrient solutions changed weekly.

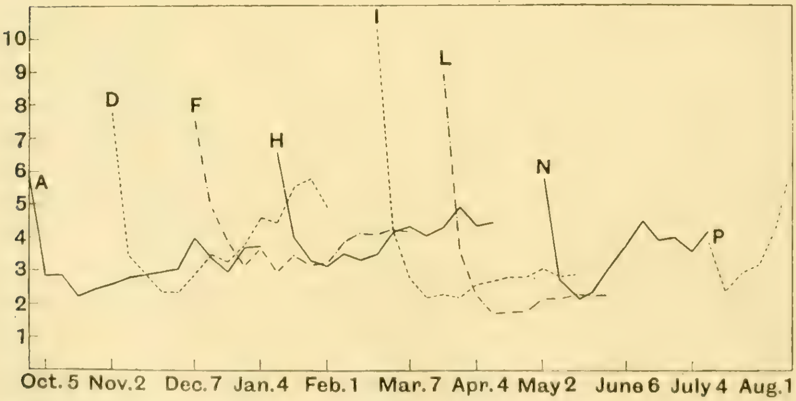


Fig. 13. Shoot/Root Ratios for weekly periods. Sept. 28th, 1915—Aug. 15th, 1916. Nutrient solutions never changed.

the production of the rootlet. In this way a great increase in absorption can be provided for with comparatively little increase in the dry weight of the root. The same structure is also the most economical for the performance of the second function of fixation, as the multitude of fine strands result in a very effective supporting agent. The shoot, on the other hand, is chiefly concerned with the processes of respiration, transpiration and assimilation. For these a considerable bulk of tissue is desirable in order to provide an adequate supply of intercellular spaces, chlorophyll and storage tissue and also that a broad surface may be presented to make the most effective use of sunlight in the elaboration of food material. In order to carry a great expanse of leaf stout stems are necessary, and consequently a large amount of material has to be used in the construction of the shoot. As the plant gets older, the root is increasing its absorbing capacity at the expense of comparatively little new material while the shoot is using up a great deal for growth and may also be acting as a storehouse of reserves, so the relative weights of the two parts tend to diverge more and more. The more rapid the growth, the more rapid the divergence, as is shown graphically by the large shoot/root ratio attained under optimum conditions.

The behaviour of root and shoot with regard to temperature is distinctly different. It has already been shown that during the first period of growth, whatever the season and the temperature, the weight of the shoot falls and then rises again, whereas the root increases steadily in weight from the beginning. After this period the temperature factor is very potent. The shoot weight at all seasons continues to rise, slowly with low mean maximum temperatures, rapidly with high mean maxima. Under no circumstances with the mean maxima attained in this experiment did the increase in dry weight of the shoot cease even for a time until the very end when growth was completed. Up to a certain limit, also, increase in the rate of shoot growth is correlated with rise of temperature. Root growth, on the other hand, is much affected by low mean maximum temperatures, and practically no advance was made in any series, irrespective of the food supply, from mid-November to January, over a period during which the mean maxima were consistently below 60° F. Rise in temperature does not have the same relative beneficial action on the root that it does on the shoot, as no sharp rises in root weight could be detected when temperatures went up. There is some indication that whereas the roots can grow satisfactorily in high temperatures when they are subjected to plenty of heat from an early period of life, root growth is severely checked or even stopped if a sudden and prolonged increase in temperature occurs when the plant is well developed, but this check in root increase does not necessarily imply a corresponding check to the shoot.

Cessation of root increase is a constant phenomenon and always occurs some time before the shoot stops growing. In some cases there is evidence that an actual decrease in weight occurs after this period but as this is most marked in the plants which are grown in constantly changed food solution it is possible that the loss may be partly due to abrasion in the mechanical process of handling, the loss not being made good by growth. Without further information it is impossible to say whether this loss of weight in the roots is of real significance.

(2) *Shoot growth and pod formation.*

As the duration of the tests was limited to a certain number of weeks few of the series reached the stage of pod formation. Of these, three received abundant food and one was limited in this respect. As soon as pod formation begins the rate of growth of the stem and leaves, excluding the reproductive organs, falls off immediately and relatively little extra weight is put on, though the increase in weight of the whole shoot is exceedingly rapid (Figs. 4 and 10). Up to the time of flowering the energy of the plant is directed to building up a healthy body capable of bearing the strain of reproduction. When seed formation begins the energy is diverted into this channel, and the shoot (stem and leaves) becomes merely the agent whereby the necessary materials for building up the fruit and seed are supplied. Consequently it is now unnecessary for more food to be expended in the production of a bigger shoot, so little increase takes place and there is evidence that at a later stage still loss of weight occurs owing to the transference of the actual substance of the stem and leaves to the seed. This transference has been proved in the case of certain other plants, among which barley and wheat may be instanced[1]. The most rapid increase in the weight of the pods occurs during the first two or three weeks after they appear, after which the increase slackens off till eventually a drop in weight may occur associated with the onset of maturation and desiccation.

(3) *Relation of nitrogen absorption to dry matter produced.*

A true estimate of the amount of nitrogen taken up can only be obtained by analysis of the plant itself, but labour difficulties during the war rendered it impossible to have the necessary analyses made. In a few series, however, the water culture solutions were sampled at intervals and the nitrogen present estimated as potassium nitrate. These figures indicate the amount of KNO_3 that had disappeared from the solutions in a given time and enable some idea to be formed of the amount of nitrate taken up and utilised by the plant in the production of varying weights of dry matter. The great objection to this method of estimating the nitrogen absorption is that the amount of nitrogen that is lost by decomposition or denitrification is probably a variable unknown quantity for which it is difficult to devise a method of determination. Tests made at various times with solutions allowed to remain in the bottles for some days or weeks without any plants growing in them seem to show a slight loss of nitrate, though this is not very considerable even after the lapse of some time. The figures obtained in the present experiments are probably sufficiently accurate to give a true indication of the trend of affairs even though the actual quantitative measure they represent cannot be fully accepted.

---

[1] (*a*) Brenchley, W. E. and Hall, A. D. (1909). "Development of the Grain of Wheat." *Journ. Agric. Sci.* III, pp. 195–217.

(*b*) Brenchley, W. E. (1912). "Development of the Grain of Barley." *Ann. Bot.* XXVI, pp. 913–928.

Analyses of the solutions for KNO_3 were made at various times in the unchanged series L and N and the changed series K and M. When the solutions were unchanged the KNO_3 available throughout the life of the plant was only ·6 gm. per plant and by the time the experiments were finished very little or none of this remained in the solutions. The results obtained in these cases are summarised in Table I, in which the figures apply to the unit of ten plants, grown in six litres of solution.

Table I (Solutions not changed).

Date	After — weeks growth	KNO_3 lost from 6 litres solution	Dry weights of 10 plants produced in period	Ratio of KNO_3 lost to dry matter produced over whole period
Series L		grams	grams	
April 21st	6	4·02	8·044	1 : 2·00
May 12th	9	5·76	14·887	1 : 2·59
May 19th	10	5·76	15·337	1 : 2·63
Series N				
May 10th	2	·96	0·359	1 : 0·37
May 17th	3	1·89	2·520	1 : 1·33
May 24th	4	3·16	7·292	1 : 2·31
June 23rd	8	5·92	23·166	1 : 3·91

The ratio column of Table I shows clearly that as the pea plant gets older the increase in dry matter produced becomes less dependent upon the amount of nitrate absorbed by the roots, and that even when very little intake is possible owing to exhaustion of the food supplies some growth can still occur by means of photosynthesis. It appears that early in life, before the high tide of assimilation is reached, the plant absorbs a relatively large amount of nutrient salts by means of the roots without producing a correspondingly large quantity of dry matter, but as time goes on increasing amounts of dry matter are formed for the same amount of absorbed nitrate. The more favourable the season for assimilation the greater the amount of dry matter ultimately produced per unit of KNO_3, as is seen from the fact that for every gram of KNO_3 3·91 gms. of dry matter were produced in series N in the summer months against 2·63 gms. in series L in late spring.

In the changed series K and M a fresh supply of nitrate was added every week and the results give the measure of absorption and growth for weekly periods, instead of extending over the whole life of the plant to date as in the former case. Under these circumstances it is to be expected that greater irregularity will occur in the figures, as the constant changes in environmental conditions will only be averaged up for a week instead of for the whole time of growth. Even so, however, there is some indication, especially in series M (Table II), that as the plant gets older relatively less nitrate is utilised in the production of dry matter, though the evidence is less conclusive than where semi-starvation occurs.

These results bring out the fact of the relative greater importance of assimilation at the time of heavy growth, when more efficient use is made by the plant of the food material absorbed by the roots. For full information on this point it would be necessary to have a series of analyses of the plant and the nutrient solution at regular intervals in order that the various factors introduced by loss, absorption and assimilation might be examined and correlated.

Table II (Solutions changed).

Date	At end of — week	KNO_3 lost in the week from 6 litres solution	Dry weights of 10 plants produced in the week	Ratio of KNO_3 lost to dry matter produced in the week
Series K		grams	grams	
April 14th	5th	2·34	3·176	1 : 1·36
,, 21st	6th	1·65	5·738	1 : 3·48
May 12th	9th	3·72	6·650	1 : 1·79
,, 19th	10th	4·14	20·984	1 : 5·07
,, 26th	11th	3·52	5·847	1 : 1·66
Series M				
May 10th	2nd	1·29	·737	1 : 0·57
,, 17th	3rd	1·89	2·409	1 : 1·27
,, 24th	4th	2·46	2·792	1 : 1·14
June 23rd	8th	4·44	16·509	1 : 3·72

SUMMARY.

1. Growth may be divided conveniently into two well-marked periods.

(*a*) 1*st period*, from the seedling stage till the time that the plant regains its initial weight after the loss by respiration, *i.e.* the time during which a casual observer would say the plant "makes no growth."

(*b*) 2*nd period*, succeeding the former, during which the plant is obviously making growth, and which continues till the latter ceases and desiccation sets in.

2. The length of the first period varies inversely with the mean maximum temperature, as the rate at which assimilation is able to make good the loss by respiration increases directly with rise of temperature, up to a certain limit.

3. The possible amount of growth as measured by the dry matter produced depends directly upon the bright sunshine and temperature when the food supply is adequate, but when the latter is limited the total growth is much less owing to the lack of material for building up the tissues. Beyond a certain limit, however, the beneficial factors of heat and bright sunshine become harmful and result in the premature death of the plant.

4. During the first period the rate of growth as shown by the efficiency index was associated with relatively warm days and nights, bright sunshine having little significant effect; the light, however, was good throughout for the season of the year. During the second period the rate was associated strongly with sunshine and warm days, but not significantly with the night temperatures, which did not fall below 32° F.

5. During the greater part of the year the maximum rate of growth (highest efficiency index) is reached early in life, very soon after the second period begins. Under favourable environmental conditions a high rate of increase is then maintained for several weeks, but in less favourable circumstances the efficiency index rapidly falls. In winter, when temperatures rule low and there is little bright sunshine, the maximum rate of growth is not reached till several weeks after the beginning of the second period, and even then the efficiency index is not very great.

6. Plants with a restricted food supply make less total growth than those with abundant food. The falling off in the amount of dry matter produced does not seem to be gradual but is marked by definite periods of which the incidence varies at different seasons.

7. Broadly speaking the response of plants to the environmental conditions is similar whether the food supply is abundant or restricted,

though the mean rate of growth is lower when food is scarce. During the first period the excess of food has no significant effect upon the rate of growth, but during the second period the mean differences in the rate of increase in the presence of abundance and of scarcity of food are strongly significant in favour of the well supplied plants.

8. During the early weeks, corresponding approximately to the first period of growth, the shoot/root ratio falls, owing to the steady increase in root weight which is associated at first with a decrease and later with an increase in shoot weight. During the second period of active growth the shoot increases in weight far more rapidly than the root, and thus the shoot/root ratio rises steadily. Increase in shoot growth is closely associated with rise in temperature, though the lowest mean maximum attained in the experiments did not cause a cessation of growth. Root growth is much affected by low mean maximum temperatures and practically ceased, under the experimental conditions, when they were consistently below 60° F. Rise in maximum temperature had much less beneficial action upon the roots than upon the shoots.

9. In early stages of growth the amount of nitrate absorbed by the plant is relatively large in comparison with the dry matter produced, but later on more dry matter is formed in proportion to the same amount of nitrate, owing to the accumulation of the products of assimilation.

In conclusion I wish to express my indebtedness to Mr R. A. Fisher, who has examined the figures and has furnished me with the statistical information embodied in this paper.

NOTE.

SOME FACTORS IN PLANT COMPETITION

(THIS *JOURNAL*, VOL. VI, NOS. 2 AND 3, 1919.)

By an oversight the weights of the barley and mustard seeds, used in the calculation of the efficiency indices, were omitted.

Mustard.	Tables I—II,	pp. 145—147.	Average wt. per seed	·007 gm.
Barley.	Tables III—VI,	pp. 149—150.	,, ,,	·055 ,,
Barley.	Tables IX—XVI,	pp. 162—167.	,, ,,	·065 ,,

In each case the efficiency indices are per cent. per day.

GLOMERELLA CINGULATA (STONEMAN) SPAULD. AND V. SCH. AND ITS CONIDIAL FORMS, *GLŒOSPORIUM PIPERATUM* E. AND E. AND *COLLETOTRICHUM NIGRUM* E. AND HALS., ON CHILLIES AND *CARICA PAPAYA*.

By JEHANGIR FARDUNJI DASTUR, M.Sc.,

Supernumerary Mycologist, Pusa.

(With Plate X.)

On chillies or peppers (*Capsicum annuum* and *C. frutescens*) three anthracnoses have been recorded to date. In 1889, Ellis described a very destructive disease in America caused by *Glœosporium piperatum* E. and E. Halstead[1], in the following year, discovered another which was considered to be different from the previous one, on account of the presence of setae in the acervuli; it was consequently named *Colletotrichum nigrum* E. and Hals. In 1913, Sydow[2] described a new species of *Vermicularia* on chillies, sent to him by Mr McRae from South India. In India, especially in Bihar and Madras, *Vermicularia Capsici* Syd. is the most destructive disease and causes a great deal of damage to the fruits and to the plants as well, at least in Bihar. The other two diseases have not as yet been reported to do much damage in India, but in Burma they seem to cause much loss of the fruits. In 1917, an experimental plot of two acres on the Pusa Farm bore a crop of chillies. The damage done to the plants and fruits by *V. Capsici* was considerable but *G. piperatum* was rarely found on fruits and *C. nigrum* was much more scarce. However, on the stem *G. piperatum* was slightly more prevalent than on the fruits but it was invariably found only on the stem attacked by *Choanephora Cucurbitarum* (B. and Rav.) Thaxter and *V. Capsici*. As a rule only mature fruits are attacked by *G. piperatum* and the other two anthracnose fungi and they produce similar discolorations. The disease is first visible as a small circular black or greenish black spot, which is generally, but not always, slightly depressed. As the infection spreads the fruit loses its normal red colour and turns whitish yellow or greenish yellow, reddish yellow or straw coloured. It also becomes prematurely dry and very brittle. However, the acervuli of *G. piperatum* can be readily distinguished from those of the other two fungi by their pink colour, especially when fresh. *Colletotrichum* and *Vermicularia* acervuli are not easily distinguishable because of the black colour due to the presence of setae; but the *Vermicularia* acervuli generally look more bristly and more erumpent as a part of the stroma is above the epidermis. Old *Glœosporium* acervuli, which have turned black, may be mistaken for *Colletotrichum* acervuli on superficial examination.

---

[1] Halstead, B. D. *Report of the Botanical Department, New Jersey Agr. Col. Exp. Stat.*, 1890, pp. 358 and 359.

[2] Sydow, H. Beiträge zur kenntnis der Pilzflora des Südlichen Ostindiens-I. *Ann. Myc.*, xi, 1913, p. 329.

The disease due to *V. Capsici* will be treated in a separate paper, so a further account of it is unnecessary.

G. piperatum *E. and E.*

The diseased part of the fruit shows slightly raised points. This is due to the development of acervuli underneath them. With the growth of the acervuli the skin is ruptured by elliptical, triangular or irregular rifts. If the diseased spot be examined with a hand-lens, crater-like structures filled with beaded or cauliflower-like pink growths are visible due to the development of spore masses. The acervuli start from the centre of the diseased spot and are generally concentrically arranged but they may also be scattered. They are, when fresh, oily and flesh pink in colour which may either change to dull light pink when they become old or to black, from margin inwards.

In the epidermal and sub-epidermal cells hyphae collect together and eventually develop into a pseudo-parenchymatous stroma; from the top of which conidiophores arise. As a rule the latter are short and conical with a tapering apex but they become much elongated and narrow under extremely moist conditions. They measure 11·0–18·7 × 2·7–4·9μ. From tips of the conidiophores spores are cut off. Under the pressure of the growth of conidiophores and development of spores the cuticle is pushed up and eventually ruptured. At first the raised cuticle keeps the conidia more or less confined underneath it and allows their escape only through a small opening but later the cuticle is completely thrown aside (Plate X, Fig. 2). It is the frayed edges of this ruptured cuticle that give the diseased part of the fruit, at times, a scaly appearance. The spores are held together in a gelatinous mass at the opening of the acervulus as in other species of this genus. They are elliptical with broad round ends, hyaline in colour and have an oil globule in the centre (Fig. 3). They measure 11·0–21 × 4·4–5·5μ.

This development of the acervulus of *G. piperatum* E. and E. is similar in all its details to that of *Colletotrichum Lindemuthianum* (Sacc. and Mag.) Br. and Cav. as described by Edgerton[1] except that in the former the stroma of pseudo-parenchymatous cells distinctly precedes the formation of conidiophores while in the latter the stroma is of a later origin.

Specimens of *Colletotrichum nigrum* E. and Hals. on chilli fruits collected in Burma and Pusa show that this fungus agrees in all characters with *G. piperatum* except that the acervuli of *C. nigrum* have long rigid dark brown setae up to 150μ long and 4μ broad.

The perfect stage of *G. piperatum* and *Colletotrichum nigrum* has not previously been recorded on the host plant but at Pusa it has been found on fruits on rare occasions. Miss Stoneman[2], who succeeded in growing in cultures the perithecial stage of *G. piperatum*, named it *Gnomoniopsis piperata* which was subsequently changed to *Glomerella piperata* (Stoneman) Spauld. and v. Sch.; and Taubenhaus[3] considers, from inoculation experiments, *Gl. rufomaculans* (Berk.) Spauld. and v. Sch., which is the same as *Gl. cingulata* (Stoneman) Spauld. and v. Sch. according to Edgerton[4], to be the perfect stage of *C. nigrum*. Butler[5] is inclined to think *Gl. piperata* (Stoneman) Spauld. and v. Sch. is synonymous with *Gl. cingulata*. The author is of opinion, for reasons given below, that *G. piperatum* and *C. nigrum* are identical and that their perithecial stage is *Gl. cingulata* (Stoneman) Spauld. and v. Sch.

Growth of Gl. piperatum *E. and E. in cultures.*

Cultures on glucose-meat-extract-agar started from conidia give for the first few generations a fairly abundant aerial growth which to begin with is white but soon turns pink owing to the development of spores. In places, the culture turns black or greenish black on account of the formation of strands of dark brown hyphae, especially at the lower end of the culture tube and at the margin of the agar medium. By continuous subculturing on agar media and on sterilized potato tubers and chilli pods the spore-bearing capacity is lost and the cultures remain sterile, and on glucose-meat-extract-agar the growth is no more aerial but matted and submerged. But if transfers from this sterile fungus are made on sterilized chilli or potato stems, the growth is again fertile; the conidia are borne on tips of hyphae and in pink acervuli; and in subcultures made on glucose-meat-extract-agar from this fertile culture the mycelium is aerial, bears conidia and the growth resembles that obtained originally from conidia planted on glucose-meat-extract-agar but after three or four generations on the same medium it again becomes sterile and confined to the substance of the medium.

---

[1] Edgerton, C. W. The Bean Anthracnose. *Louisiana Agric. Expt. Sta. Bull.*, 119, April, 1910, p. 5.

[2] Stoneman, B. A comparative Study of the Development of some Anthracnoses. *Bot. Gaz.*, XXVI, p. 104, 1898.

[3] Taubenhaus, J. J. A further Study of some Glœosporiums and their Relation to a Sweet Pea Disease. *Phytopathology*, II, No. 4, p. 159, 1912.

[4] Edgerton, C. W. The Physiology and Development of some Anthracnoses. *Bot. Gaz.*, XLV, p. 401, 1908.

[5] Butler, E. J. *Fungi and Disease in Plants*, p. 355, 1918.

The mycelium is generally composed of two kinds of hyphae, one very thin and the other very broad, closely septate and highly vacuolate. At times intercalary vesicles are formed in the hyphae. The hyphae, both broad and thin, often get fused together and form a network.

The conidia are developed either in acervuli, as in Melanconiaceae or on the tips of lateral branches of hyphae, as in Hyphomycetes. The acervulus in cultures originates as an aggregation of hyphae forming a stroma which from its commencement is brown like that of an acervulus on the host plant. From the stromatic cells hyaline basidia or conidiophores are developed from the tips of which conidia are produced in succession. The stroma is usually without appendages but at times it bears brown hyphae, generally flexuous, rarely rather stiff. These appendages have some remote resemblance to the setae of a *Colletotrichum* acervulus.

The spores, when sown in water, swell before germinating. At times only a part of the spore is swollen, the unswollen end having a pinched-in appearance. The germinating spore (Fig. 3) may become septate. The germ-tube is developed from either end or from both the ends. Appressoria are formed at the tips of the germ-tubes. The germ-tubes occasionally bear secondary conidia. Germinating spores may get fused together by their germ-tubes or branches arising therefrom.

In cultures, sclerotia are often developed. They are generally small and round but at times they have been observed to be as big as 1 mm. in diameter. In cross sections these sclerotia are found either to be a homogeneous mass of hexagonal or rectangular brown cells, or to be slightly differentiated into cortex and medulla, the central cells being large and thin-walled while the peripheral cells have a smaller lumen and thicker walls.

Glomerella *stage.*

Shear and Wood have found that if a culture from any particular acervulus or group of acervuli does not produce the ascogenous stage on corn meal at 75° to 85° F., it is useless to experiment further with material from the source[1]; and they are of opinion that the perithecial forming faculty in the numerous cases of *Glomerella* studied by them is a fairly fixed hereditary character; because if once a race or strain which produces perithecia in culture media is obtained other generations from this strain or race continue to produce perithecia indefinitely[2].

Edgerton considers corn-meal-agar the most satisfactory medium for the growth of the fungi belonging to the genus *Glomerella.*

Krüger[3] has found partly sterilized potato stems as particularly suitable for the development of perithecia. These and various other media have been tried for the development of the ascogenous stage not only of the chilli fungus but also of the *Carica papaya* anthracnose. It seems to me doubtful if the medium has any direct influence on the development of perithecia. What seems to be most essential is that a race or strain should be capable of producing the perfect stage. If once such a race or strain is obtained perithecia are formed on almost any medium, especially solid, at least for the first few generations. As will be seen later the perithecia forming faculty is not a fixed hereditary character which would ensure the development of perithecia indefinitely, as stated by Shear and Wood. Perithecial strains completely lose their spore-bearing faculty when their successive generations are cultivated for some length of time on the same medium and at room temperature. But, however, these sterile strains can be induced to form asexual spores by sudden change of food or temperature, *e.g.*, subcultures on corn-meal, corn-meal-agar or sterilized chilli stem produce the conidial form when the transfers are made from a strain that has become sterile, through several generations having been cultivated on glucose-meat-extract-agar. Subcultures from sterile cultures on glucose-meat-extract-agar at room temperature, at times, develop the conidial form if they are kept in a hot incubator at 90° F. in winter, and in a cold incubator at 66° F. in summer. If three or four successive generations of these conidia-producing cultures are cultivated on the same food and under the same conditions, they again become sterile. But, though the lost conidial form can be recovered, so far all attempts to get back the perithecial form from the strain which has lost it have been unsuccessful. What factor or factors influence the development of the perfect stage is not known.

---

[1] Shear, C. L. and Wood, A. K. Ascogenous Forms of *Glœosporium* and *Colletotrichum. Bot. Gaz.*, XLIII, p. 262, 1907.

[2] Shear, C. L. and Wood, A. K. Studies of Fungous Parasites belonging to the Genus *Glomerella. U.S. Dept. Agric., Bur. Pl. Industry, Bull.*, No. 252, p. 72, 1913.

[3] Krüger, F. Beiträge zur kenntnis einiger *Glœosporium* I und II. *Arb. Kais. Biol. Anst. f. Land-u. Forstwirtschaft,* IX, 2, p. 217, 1917.

Since 1914, *Glœosporium piperatum* E. and E. has been obtained in cultures on several occasions and cultivated on numerous kinds of media but the perithecial stage has been developed only on two occasions. In April 1915, perithecia were first formed on partly sterilized chilli stems. But unfortunately this strain was allowed to die out. In December of 1918, cultures of *G. piperatum* were taken from diseased chilli fruits in Burma by Babu P. C. Kar, Fieldman to the Imperial Mycologist, to whom my acknowledgements are due. Cultures on glucose-meat-extract-agar and on corn meal produced both the perithecial and *Glœosporium* forms at Pusa.

In the winter of 1916, the *Glomerella* stage was for the first time observed on diseased chilli fruits; a few fruits attacked by *Glœosporium piperatum* were incubated. The concentric rings of shining oily pink acervuli on one of the fruits were replaced in five or six days by an undulating, black, rugged crust in which were found the perithecia. In 1917 and 1918 perithecia were again found on a few incubated fruits attacked by *Glœosporium piperatum.*

The perithecial form found on these incubated fruits was identical with that previously produced in cultures of *Glœosporium piperatum* on partly sterilized chilli stems and on glucose-meat-extract-agar and that described by Miss Stoneman.

The perithecia found on the fruits (Fig. 4) are caespitose, membranaceous, pear-shaped with a short neck, dark brown in colour—light coloured towards the ostiole—situated on, or partly immersed in, a stroma of loosely inter-woven hyphae. They are not hairy, but the neck in some cases is slightly tufted. The perithecia resemble those of *Glomerella piperata* described by Miss Stoneman except that they are not hairy as figured by her.

Cultures taken from diseased fruits bearing perithecia have given the ascogenous stage. On maize-agar the perithecia are either scattered or aggregated together forming big black nodules like those of *G. frustigena* (Clint.) Sacc.[1]. These on sectioning are found to be somewhat differentiated into cortex and medulla. The cortex is composed of large thin-walled cells lightly coloured, while dark-coloured small cells, compactly packed, form the medulla. Embedded in these nodules are perithecia in one or more layers.

---

[1] Edgerton, C. W. The Physiology and Development of some Anthracnoses. *Bot. Gaz.*, XLV, p. 387, 1908.

In cultures the neck of the perithecium varies a great deal in length, it may be almost absent or as long as that figured by Miss Stoneman. Between these extremes there are all degrees of variation in the size of the neck. There is the same variation in the hairiness of the neck. It may be entirely smooth or it may have hairs sticking out from its sides in varying quantities. These characters are not constant even on the same medium and in the same cultures.

The asci are hyaline, sessile and as a rule clavate. The asci (Fig. 5 *c*) from the host generally measure between 45·0–66·0 × 7·7–11·0μ; but on a fruit collected in November of 1918 the range of variation was between 49·5–93·5 × 6·6–9·9μ. In the bigger asci the ascospores were arranged in a single row, one below the other (Fig. 5 *b*). In cultures there is the same range of variation in shape and size as that found by Shear and Wood[1] in the asci of *Glomerella rufomaculans* (Berk.) Spauld. and v. Sch. (= *Glomerella cingulata*). The ascospores (Fig. 7) are eight in number, hyaline, slightly curved, elliptical and generally subdistichous, they measure 12·0–19·0 × 4·4–6·6μ. They are quickly shed after maturity; the ascus wall rapidly disintegrates and the spores ooze out of the neck of the perithecium where they are held together in a drop of a shining viscous liquid. The ascospores germinate in water by giving out a germ-tube from near one of the ends; they may, at times, become septate; but they do not anastomose as do the conidia (Fig. 8). The germ-tubes after growing for some distance form an appressorium at the tip.

In old perithecia (from the host or from cultures) ascospores are found to lie scattered or in groups of eight as in the ascus but without the ascus wall which is invariably dissolved. They have, as a rule, become septate, generally once rarely twice, and their wall has distinctly turned pale brown. Ascospores that have germinated in the perithecium have been at times observed to have anastomosed by their germ-tubes. As already stated ascospores sown in water have not shown any of these changes even when kept for any length of time.

Miss Stoneman[2] who referred the perfect forms of *Glœosporium* and *Colletotrichum* to a new genus, *Gnomoniopsis*, is inclined to consider it as aparaphysate; von Schrenk and Spaulding[1] who later changed this name to *Glomerella* also describe it as aparaphysate; to Edgerton[2] it seems best to regard this genus as such; but Sheldon[3] has seen paraphyses in a number of forms and Shear has found the asci of *G. rufomaculans* var. *vaccinii* Shear to be accompanied by what seem to be evanescent paraphyses. In the perithecia of chilli *Glomerella* are found at times sterile bodies (Fig. 5 *a*) of varying length and breadth but never longer or broader than the normal asci. They are not completely filled with protoplasm. It has, as a rule, contracted from the walls and become collected in the centre of these bodies. They can not be regarded as paraphyses because they seem to be asci which have become abortive at various stages of their development.

---

[1] Shear, C. L. and Wood, A. K. Ascogenous Forms of *Glœosporium* and *Colletotrichum*. *Bot. Gaz.*, XLIII, No. 4, p. 263, 1907.

[2] Stoneman, B. A comparative Study of the Development of some Anthracnoses. *Bot. Gaz.*, XXVI, pp. 99–114, 1898.

Miss Stoneman[4] considers the perithecial form of *Glœosporium piperatum* E. and E. to closely resemble *Gnomoniopsis* (*Glomerella*) *cingulata* but makes a new species of the former as she finds a specific difference in its more slender perithecia and smaller spore measurements. At the same time she admits that these characters vary in different cultures and that the larger measurements of the perithecial stage of *G. piperatum* are common to smaller perithecia and spores of the privet anthracnose.

Miss Stoneman also lays importance to the difference in growth on nutrient media of the colonies from ascospores and conidia of the chilli and privet anthracnoses. From the later investigations of Edgerton[5] and Shear and Wood[6] it seems clear that much reliance should not be put on cultural characters for the determination of *Glomerella* species as they have found the perfect stage to be extremely variable.

That cultural characteristics and spore measurements are not a safe criterion in determining specific differences is also evident from the present study of the *Glomerella* on chilli. As already stated the perithecia and asci (Figs. 5 and 6) vary a great deal in size and shape; in many cultures the measurements of the asci and ascospores reached the limits given by Miss Stoneman for *G. cingulata*. It seems therefore that there are not sufficient reasons to consider the ascogenous stage of *Glœosporium piperatum* E. and E. to be different from *Glomerella cingulata* (Stoneman) Spauld. and v. Sch.

---

[1] Schrenk, H. von and Spaulding, P. The Bitter-Rot of the Apple. *U.S. Dept. of Agr., Bur. of Pl. Ind., Bull.*, No. 44, p. 29, 1903.

[2] Edgerton, C. W. The Physiology and Development of some Anthracnoses. *Bot. Gaz.*, XLV, p. 389, 1908.

[3] Sheldon, J. L. The Ripe Rot or Mummy Disease of Guavas. *West Virginia Agr. Expt. Sta. Bull.*, No. 104, p. 312, 1906.

[4] Stoneman, B. *loc. cit.*, p. 106.

[5] Edgerton, C. W. *loc. cit.*, pp. 393–396.

[6] Shear, C. L. and Wood, A. K. Studies of Fungous Parasites belonging to the Genus *Glomerella*. *U.S. Dept. of Agr., Bur. of Pl. Ind., Bull.*, No. 252, pp. 65 and 98, 1913.

Development of Glœosporium *and* Colletotrichum *acervuli in cultures of* Glomerella.

In December 1918, a chilli fruit was found attacked by *Glœosporium piperatum* E. and E.; a week after it was incubated, the shining pink acervuli were replaced by a black, corrugated, rugged, carbonaceous crust. In this crust was found the ascogenous stage. A small bit from this perithecial crust was planted in a tube of glucose-meat-extract-agar. The growth remained sterile. In sub-cultures from this culture (which we shall call A) on sterilized chilli stems and on maize-meal-agar, conidia and perithecia were produced, but setae were invariably absent; but, however, sub-cultures on glucose-meat-extract-agar were sterile. Four months later, *i.e.* in April of the following year, sub-cultures from the sterile culture A were made on sterilized chilli stems (culture B) and on glucose-meat-extract-agar (culture C). In B the perithecial stage was produced, but not the conidial; while in C acervuli with or without setae were developed but no perithecia.

Thus all of a sudden the original sterile culture broke up into two different strains, one producing only perithecia on sterilized chilli stems and the other forming acervuli with and without setae on glucose-meat-extract-agar. These strains remained distinct only for a short time. The conidial strain soon lost its setae-producing faculty and developed the perithecia-forming faculty on glucose-meat-extract-agar. Subsequent sub-cultures on glucose-meat-extract-agar from these two strains were identical.

Sub-cultures from the perithecial strain, culture B, continued to produce perithecia, at first along with the *Glœosporium* stage, on various media, including glucose-meat-extract-agar. Eventually this strain produced only the perfect stage, without the conidial.

Sub-cultures from the conidial strain, culture C, on sterilized chilli stems, oat-juice-agar and maize-agar, at first, gave both the perithecial stage and the conidial, either with or without setae, but later only the perfect stage was produced on these media. Sub-cultures on glucose-meat-extract-agar, ± 5 Fuller's scale and neutral, and on bouillon agar, gave for some time only the conidial stage with and without setae. This tendency of developing only the conidial stage was lost by continuous sub-culturing on glucose-meat-extract-agar, and that of forming the perfect stage was developed. Sub-cultures from the original culture C, taken after a lapse of 2, 3, and 10 months on glucose-meat-extract-agar and other agar media, gave only the perithecial stage. Single spore cultures of ascospores and asci have produced only the perithecial stage, the conidial being absent.

From the behaviour of the chilli *Glomerella* in cultures it appears that *Colletotrichum nigrum* and *Glœosporium piperatum* are one and the same fungus, the conidial stage being generally without setae in Bihar (either the setae are developed only under certain conditions or only certain strains are capable of producing setae). The development of setae is not a constant feature of the genus *Colletotrichum.* The well-known bean disease *C. Lindemuthianum* forms pustules very often without the least trace of setae; in fact this bean anthracnose was first put in the genus *Glœosporium.* The same is true of the anthracnose on cucurbits. It was first named *G. lagenarium* but when setae were later found it was placed in the genus *Colletotrichum.* The anthracnose of tomatoes Chester[1] described in 1891 as caused by *C. lycopersici* n.sp. as there was an abundant development of setae in the acervuli, but in the following year the diseased spots were without setae and to all appearance the fungus was a *Glœosporium* and therefore Chester raises the question whether the presence or absence of setae is of sufficient generic importance to separate the two genera. Edgerton[2] considers the distinction between the *Glœosporium* and *Colletotrichum* so poor that he prefers to drop the name *Colletotrichum* in favour of *Glœosporium* in his discussion on the development of anthracnoses. According to Krüger[3] *Colletotrichum* and *Glœosporium* cannot be sharply divided into two distinct genera and therefore he considers *Colletotrichum* as a sub-genus. Miss Stoneman[4] has found the presence of setae so variable as to doubt whether they form a well-founded basis for distinguishing these two genera. Shear and Wood[5] are also of the same opinion. They have found setae in the acervuli in one part of a pure culture, whereas in other parts of the same culture they were absent. They[6] have also found this same variation occurring upon leaves, especially in the form found upon cranberry.

---

[1] Chester, F. D. *Delaware Station Report for* 1891, pp. 60–63 and for 1892, p. 80.

[2] Edgerton, C. W. *Loc. cit.*, p. 369.

[3] Krüger, F. *Loc. cit.*, p. 303.

[4] Stoneman, B. *Loc. cit.*, p. 70.

[5] Shear, C. L. and Wood, A. K. Ascogenous Forms of *Glœosporium* and *Colletotrichum. Bot. Gaz.*, XLIII, p. 263, 1907.

[6] Shear, C. L. and Wood, A. K. Studies of Fungous Parasites belonging to the Genus *Glomerella. U.S. Dept. Agr., Bur. Pl. Ind., Bull.*, No. 252, p. 64, 1913.

Even in single-spore cultures some acervuli show many setae, others a few and still others none.

Colletotrichum nigrum *E. and Hals.*

The acervuli of *C. nigrum* E. and Hals. on chilli fruits collected in Burma and in Pusa are quite similar to those of *G. piperatum* E. and E. already described, except that in the acervuli of the former there is a development of stiff, erect dark brown setae, which measure up to 150μ long and 4μ broad.

In December 1918, a chilli fruit was found in Pusa attacked by *C. nigrum*. The acervuli were carefully examined under a binocular microscope and all of them, without exception, were found to have developed setae. Four series of cultures from this diseased fruit were started on glucose-meat-extract-agar.

1. A single conidium was planted on the medium.

2. A diseased seed was aseptically removed and transferred to the medium.

3. It may perhaps be suspected that the fruit might have been infected with *G. piperatum* E. and E. as well, the acervuli of which had escaped detection under the microscope, that the single conidium might have been taken from a *Glœosporium* acervulus and that in the tissues of the diseased seed both *Glœosporium* and *Colletotrichum* hyphae might be present. To be sure that only *C. nigrum* was really taken in culture a single seta was picked off and planted on the medium.

4. The infected fruit was incubated and in less than a week a thick, black, undulating crust was formed where there were originally acervuli of *C. nigrum*. In this crust were found perithecia. A single ascus was transplanted on the medium. (This development of the perfect stage is similar to that already described in the case of *G. piperatum*.)

A fifth series was at the same time started, for comparison, from a single ascus got from a fruit originally attacked by *G. piperatum* E. and E. and which had developed the ascogenous stage on incubation.

At room temperature, which ranged between 62° to 68° F., the growth in all these five series of cultures was alike. The mycelium was matted and confined to the substance of the medium and at first the colour of the mycelium on the surface of the slant was distinctly pink, but there was no development of conidia except in the culture started from a single seta, Ser. 3rd; there were no setae in this culture. The pink colour was soon replaced by black or greenish black. In a week's time the surface of the medium was covered by a thick undulating black crust, punctuated by small raised dots or pinheads; this crust was the stroma in which were wholly or partly immersed perithecia. In later subcultures, the pink colour of the young mycelium was completely absent.

A second lot of cultures from the above five series was at the same time incubated at a temperature of 89·6° F. The growth in all these cultures was again identical but different from that described above. On the upper drier part of the medium it was fluffy, but on the rest of the slant the growth was slightly aerial and the aerial mycelium had formed white feathery strands. The colour of the slant was distinctly pink, relieved occasionally by appressed black strands or black dots, which were immature perithecia. On the sides of the medium there was a development of black stroma which contained acervuli without setae, conidia were also produced on the tips of hyphae but in no part of the cultures were setae developed. The acervuli and conidia were similar to those of *G. piperatum* E. and E.

In cultures on corn meal at first the conidial stage was developed which was later replaced by the perithecial; all these cultures were identical in appearance but the one originally started from a single seta formed setae in some of the acervuli which were produced in large numbers while in the other cultures acervuli were few and without setae.

The perithecia and asci on the host and in cultures are exactly similar to those already described. They show the same range of variation as regards the size and hairiness of the perithecial neck and the size of the asci as that shown by the perithecia and asci of *Glomerella cingulata* (Stoneman) Spauld. and v. Sch., the perfect stage of *Glœosporium piperatum*. The asci (Fig. 14) from the host measure 44·0–82·5 × 9·9–12·1μ, and the ascospores measure 15·4–19·8 × 5·5–6·6μ. The asci are slightly bigger than those generally found on the chilli fruits infected by *G. piperatum* but they are of the same size as those found on a fruit last year (cf. Fig. 4). The bigger size of the asci is due to the disposition of the ascospores in a single row one below the other.

The ascospores in size and shape are similar to those already described; in old perithecia the ascospores have been found to have become septate and to have coloured brown.

The fungus grows luxuriantly in winter at room temperature—62° to 69° F.—and develops perithecia but the ascospores do not germinate either in water or in nutrient media at this temperature; however they readily do so when incubated at 89·6° F.

With the development of the perithecial stage, *Glomerella cingulata*, from *Colletotrichum nigrum* E. and Hals. the life-cycle of *G. cingulata* has been completed. We have seen that

(1) *Glomerella cingulata* has been produced in cultures of *Glœosporium piperatum* E. and E. on partly sterilized chilli stems.

(2) Acervuli with and without setae, *i.e. Colletotrichum* and *Glœosporium* forms, and the perithecial stage have been formed in cultures started originally from a perithecium from a chilli fruit which developed the perfect stage after it had first been attacked by *Glœosporium piperatum*.

(3) Acervuli without setae and the perithecial stage, identical with *Glomerella cingulata*, have been formed in cultures started from (*a*) a single conidium of *Colletotrichum nigrum* E. and Hals. and (*b*) a single ascospore from the perithecial stage developed after incubating the chilli fruit attacked by *C. nigrum*; and acervuli with and without setae and perithecia have been produced in cultures started from a single seta of *C. nigrum*. Therefore, now there seems to be no doubt that *G. piperatum* and *C. nigrum* are forms of the same fungus and that the ascogenous stage is *Glomerella cingulata* (Stoneman) Spauld. and v. Sch.

That *Colletotrichum* and *Glœosporium* on chillies are one and the same fungus is also seen from the study of the conidial forms of the *Glomerella* on *Carica papaya*, which is identical with the chilli *Glomerella*. Single spore cultures started from *Glœosporium* and *Colletotrichum* acervuli have given identical growth; in both these cultures the perithecial stage and the conidial without setae were developed. In subsequent subcultures the conidial stage was lost. Cultures started from single asci and single ascospores have produced only the perithecial stage, as in the case of the chilli *Glomerella*.

Variability of the fungus.

The strains obtained from fruits attacked by *Glœosporium piperatum* E. and E. have been cultivated on various media and under varying conditions for months on end but very great or sudden variations have never been observed. As already stated, by continuous subculturing on glucose-meat-extract-agar the conidia bearing faculty was gradually lost and the cultures became sterile. But if these sterile cultures were transferred to sterilized chilli stems, the conidia forming capacity was regained and in subsequent transfers on glucose-meat-extract-agar conidia were formed for two or three successive generations after which the fungus again became sterile. It was however found that this process of getting the conidial stage could not be carried on indefinitely. The loss of the conidia bearing faculty was ultimately complete and transfers on sterilized chilli stems gave only sterile aerial growth. But in the cultures made from the perithecial strain of *Glœosporium piperatum* incredibly large and very often sudden variations have been obtained as will be seen from the account given below. Such large variations have been observed by Edgerton[1] as well in cultures of *Glomerella* causing the bitter rot of apples. These variations consist of the absence or presence of perithecia, absence or presence of acervuli, absence or presence of setae and development of aerial hyphae or of hyphae matter and confined to the substance of the medium.

In subcultures on sterilized chilli stems and maize-meal-agar from the original sterile culture, which we have called A on page 253, acervuli without setae and perithecia were freely formed, and subcultures on glucose-meat-extract-agar from these perithecia bearing cultures also gave the perfect form in addition to the *Glœosporium* form. But in subcultures on glucose-meat-extract-agar direct from the sterile culture A the growth was sterile and confined to the surface. On the 30th of April and 2nd of May, 1917, two subcultures, GIC_1 and GIC_2, were made on glucose-meat-extract-agar from the original sterile culture A of December 1916. The first sudden variation or mutation was obtained in these subcultures. The growth in both was similar to each other but was radically different from that of the parent culture. In these cultures a black stroma was produced in which were formed acervuli with and without setae. No perithecia were produced. From GIC_1 a subculture, GIC_3, was made on the same medium on 7th May, 1917, and it was similar to its immediate parent. These three series were kept going for a long time. They showed remarkable variations from time to time. For the first two or three months they continued to produce the conidial form, but they lost this as suddenly as they gained it, and it was replaced by the perithecial stage.

GIC_1 continued to produce perithecia on glucose-meat-extract-agar till March 1918. In a subculture made on the same medium on the 16th of that month a culture two months old only acervuli with and without setae were formed and not perithecia. In the subsequent three or four subcultures the conidia continued to be formed but this stage was suddenly lost in the subculture made in the end of April. The fungus in this subculture was sterile but the growth was not similar to the original sterile culture A, but was similar to the sterile culture of *Glœosporium piperatum*. The aerial growth was moderate and covered a black or greenish black stromatic substratum formed on the surface of the medium. Subsequent subcultures on glucose-meat-extract-agar remained sterile —these cultures were kept running for over a year; but in April, 1918, subcultures on sterilized chilli stems and on corn-meal-agar perithecia were developed but not acervuli. A subculture on glucose-meat-extract-agar from the perithecia-bearing culture on sterilized chilli stems gave only the conidial stage without setae; but transfers on glucose-meat-extract-agar from the perithecial culture on corn-meal-agar were sterile. From this sterile culture transfers were made in May, 1918, on a liquid medium containing $(NH)_4NO_3$ (1 per cent.), $KH_2(PO)_4$ (·5 per cent.), NaCl (·6 per cent.), $MgSO_4$ (·25 per cent.), traces of $FeCl_2$, $CaCl_2$ and $MnSO_4$ and Glucose (3 per cent.) in 100 c.c. of water. On the surface of the liquid a thick crust pink and black in colour was formed; no fructification was produced. A subculture from this on glucose-meat-extract-agar produced pink acervuli. Setae were exceedingly rare. A culture grown on glucose-meat-extract-agar started from the sterile culture on the same medium, two months old, on the 8th May produced acervuli with setae embedded in a dark black stroma.

---

[1] Edgerton, C. W. Physiology and Development of some Anthracnoses. *Bot. Gaz.*, XLV, p. 395, 1908.

On brinjals inoculated in June, 1918, with the sterile culture perithecia were produced. Subcultures on corn-meal in April, 1919, from the sterile culture on glucose-meat-extract-agar which was kept running for a year, acervuli with and without setae were found but no perithecia. In subcultures on glucose-meat-extract-agar from the culture on corn-meal in April, 1919, acervuli with and without setae were produced. On corn-meal-agar subculture made in June, 1919, gave acervuli with and without setae.

From one of the perithecia-bearing cultures of GIC_2 subculture was made on bouillon agar on the 21st February, 1918: the resulting growth was sterile. From this sterile growth a transfer was made on glucose-meat-extract-agar. The growth of the fungus in this subculture was identical with that of the sterile fungus in the original culture A. In subsequent transfers on glucose-meat-extract-agar the fungus was sterile and formed matted hyphae on the surface of the medium; greenish black strands of hyphae, especially near about the inoculum, were developed. On chilli seedlings aseptically grown in tubes on moist cotton plugs inoculated with this sterile fungus perithecia were produced. On corn-meal-agar inoculated on the 24th April, 1918, perithecia and acervuli without setae were developed, while on sterilized chilli stems inoculated at the same time and from the same culture only sterile aerial growth was obtained. Subculture on glucose-meat-extract-agar made on the 7th

May from the fertile growth on corn-meal-agar was sterile. In a liquid medium containing $(NH)_4NO_3$ (1 per cent.), $KH_2(PO)_4$ (·5 per cent.), $MgSO_4$ (·25 per cent.), traces of $FeCl_2$ and $MnSO_4$ and maltose (3 per cent.) in 100 c.c. of water, inoculated with the sterile strain, the growth was sterile but the subculture from this, made on the 2nd May on glucose-meat-extract-agar, gave acervuli without setae. From this fertile strain the next generation on the same medium also developed acervuli without setae, but in the subsequent subcultures no fructification was developed.

In April, 1919, subcultures on corn-meal from the original sterile culture on glucose-meat-extract-agar which was kept going for a year were sterile but were not in appearance different from the cultures GIC_1 and GIC_3 of the same date on the same medium. Subcultures in May, 1919, on glucose-meat-extract-agar, were sterile: there was stroma formation from which setae were developed but no conidia. On corn-meal-agar acervuli with and without setae were produced.

GIC_3, which was a direct progeny of GIC_1, continued to develop perithecia longer than its ancestor and it did not lose the perithecial forming capacity on glucose-meat-extract-agar as suddenly as GIC_1 and GIC_2. In subcultures made in February and March, 1918, perithecia were not produced all over the agar medium as in the previous cultures but they were confined to the neighbourhood of the inoculum and their presence was marked by a dendritic growth of the perithecial stroma. As the inoculum was generally placed on the upper and therefore drier part of the slant, it was supposed that the amount of moisture determined the perithecial formation. To verify this supposition some slants were inoculated on the lower moist part and some on the drier upper part. One set of these inoculations were placed in a moist chamber in order to keep the moisture even and a duplicate set which served as a check was kept under ordinary conditions. The growth of the perithecia in both these sets continued to be poor and to be confined to near about the inoculum. In the subculture on glucose-meat-extract-agar made in the beginning of April, 1918, the perithecia were absent and the growth was sterile. But in the subculture made from this sterile race on the 24th of the same month there was a copious formation of acervuli with and without setae, but there were no perithecia. The next generation from this acervuli-producing fungus was sterile though it had all the appearance of the culture-bearing perithecia; subsequent subcultures on glucose-meat-extract-agar continued to produce conidia for only a year; setae were absent. The perithecia-forming faculty on this medium was completely lost. From the sterile culture of April subcultures were grown on corn-meal-agar on the 24th April, 1918. Perithecia were abundantly formed; in the subculture from this perithecial race on glucose-meat-extract-agar the growth was again sterile. Inoculations on sterilized chilli stems and living chilli seedlings aseptically grown in tubes on moist cotton plugs gave a copious crop of perithecia, while on brinjals and peaches only acervuli without setae were developed. Subcultures on glucose-meat-extract-agar in May, 1918, from the perithecial strain on sterilized chilli stems gave only the conidial form without setae.

Subcultures on corn-meal, in April, 1919, from the fungus cultivated for over a year on glucose-meat-extract-agar developed only acervuli with and without setae, and in transfers on glucose-meat-extract-agar acervuli with and without setae were produced but not the perfect form. Subcultures in June, 1919, on corn-meal-agar gave only conidia without setae.

INOCULATION EXPERIMENTS.

It seems doubtful if inoculation experiments are of much value in establishing the relationship of the chilli *Glomerella* with the other species of this genus or in finding the range of hosts of the chilli fungus, as the success or failure of inoculations depends on so many factors, all of which may not be controllable. Different strains or races vary not a little in virulence, *e.g.*, three strains isolated from a culture, originally started by planting perithecia on a nutrient medium, viz., (1) conidial, (2) sterile, (3) perithecial, showed distinct variations in their effects on chilli seedlings grown aseptically on moist cotton plugs in tubes. The perithecial race killed the seedlings in a fortnight and the sterile acted more slowly; and in both cases perithecia were developed on the inoculated seedlings; the conidial strain, however, infected the seedlings very slightly and no fructification was produced, even in three weeks. But the strain taken in culture from diseased fruits giving only the *Glœosporium* stage, which develops in nutrient media only this conidial form, has more virulent infecting power than the strain got from perithecia. Not only is there variation in the virulence of the different strains but there is also variation in the susceptibility of the host, *e.g.* inoculations on banana fruits have given varying results, some fruits being more readily infected than others. Conditions of temperature and moisture also play an important part in the successful inoculation of the host. Again, in the experiments in which fruits were used for the inoculation experiments it was at times difficult to decide if the fungus was growing on the inoculated host as a parasite or on account of its loss of vitality the fruit merely served as a nutrient medium for the saprophytic growth of the fungus, *e.g.* the *Glœosporium* strain was inoculated on apples through a puncture. In four days a slight brown depression round the inoculum was visible but the infection showed signs of increasing only after 25 days and a few days later the major part of the fruit was sunken and brown, the diseased area showed acervuli of the *Glœosporium* type. These results of the inoculation can be interpreted in two ways, (1) the infection had really occurred as was shown by the brown depression, but the fungus did not develop further at the time for lack of proper temperature or moisture, (2) the slight brown depression was due to the death of the cells as a result of the puncture and the hyphae had entered the cells after they were dead, and only when the vitality of the fruit was impaired by long storage was the fungus able to grow further.

This great variability in virulence is found not only in the *Glomerella* of the chilli but it seems to be a characteristic of this genus, judging from the researches of Barrus[1], and Shear and Wood[2].

The results of the inoculations are given below. In all these experiments conidia or mycelium from the cultures giving only the *Glœosporium* stage and originally started from a single spore taken from a *Glœosporium* acervulus from a diseased chilli fruit were used, unless where otherwise stated.

Chillies.

Inoculations on fruits have been made on various occasions and the results have not been uniform. Wound inoculations take more readily than surface inoculations and fruits almost ripe or wholly ripe are more susceptible than unripe fruits. The local varieties are more susceptible than the Peshawar variety. As a rule, in a couple of days after the inoculation of the fruit with the *Glœosporium* form, a black depression is produced round the inoculum which increases in size concentrically. At first pink acervuli are formed in the black depression but later they appear even beyond the discoloured area. Sometimes there is no external sign of the inoculation having succeeded till small raised points appear on the red surface of the fruit. These raised points are the immature acervuli. In some cases the infection remained very localised.

[1] Barrus, M. F. Variation of Varieties of Beans in their Susceptibility to Anthracnose. *Phytopathology*, I, No. 6, p. 195, 1911.

[2] Shear, C. L. and Wood, A. K. Studies of Fungous Parasites belonging to the Genus *Glomerella*. *U.S. Dept. of Agr., Bul. Pl. Ind., Bull.*, No. 252, p. 74, 1913.

When the perithecial form or the sterile and the conidial strains (forming acervuli with and without setae) developed from the perithecial form were used for inoculating fruits the infection took very slowly. At times immature perithecia or sclerotia were developed a week or ten days after the fruits were inoculated; acervuli with and without setae were formed only in isolated cases. At times the infection remained confined to a very limited area round the inoculum. In some cases where the infection had spread almost over the whole fruit (as was evident from the discoloration of the skin and the seeds and the presence of hyphae in the loculi of the fruits) still no sort of fructification was developed. In some cases the inoculations had completely failed. Even in the same set of experiments there were varying degrees of the extent of the infection.

Microtome section of inoculated chilli fruits show that the hyphae or germ-tube can penetrate unbroken cuticle. An appressorium is formed at the tips of an hypha or germ-tube. This appressorium lies closely appressed to the cuticle and puts forth a very fine process or germ-tube which is capable of piercing the cuticle. The process within the cuticle either remain fine or becomes swollen (Fig. 1).

Inoculations on growing points of mature plants and flower-buds and flowers were tried only with the strain giving the *Glœosporium* stage; growing points were only slightly infected and that too only under extremely moist conditions. Flower-buds and flowers were readily infected but the infection did not spread beyond the flower-stalk: acervuli were formed in a few days after inoculation.

Inoculations on seedlings grown aseptically on sterilized cotton plugs have already been described above.

Carica papaya.

Flowers and very small fruits, those that have not turned green, take the infection very readily. The first sign of successful infection on the flower is evident by the browning of the tissues in the neighbourhood of the inoculum. This browning extends very rapidly and the whole flower is soon covered with *Glœosporium* acervuli. On the fruits which are whitish yellow in colour or are just beginning to turn yellow successful inoculations have been secured through the scars of the fallen floral leaves or through the decaying styles. At the point of inoculation a circular depression is noticeable in twenty-four hours. This depression extends concentrically and in three or four days the whole fruit is infected. Fruits that have just turned green take the infection only through wounds, and that too not very readily. From the infected tissues latex exudes in tiny drops. Larger fruits could not be inoculated. When the strain that produces only the *Glœosporium* stage was used for inoculations, *Glœosporium* acervuli were developed on the infected tissues, but if the perithecial strain was used, generally either immature perithecia or sclerotia were formed, rarely acervuli.

Pods of *Dolichos lablab* and *Vigna catjang* take the infection through wounds. At times, the infection at first remains localised for some days and then spreads further.

Mature fruits of tomatoes and brinjals have been inoculated through wounds. As the result of the inoculation soft rot was produced. Brinjals were inoculated with the *Glœosporium* form and the perithecial. In both cases *Glœosporium* acervuli were produced.

Inoculations with apples have been partially successful as stated above. Ripe fruits of peach have been successfully inoculated with the perithecial form. *Glœosporium* acervuli were formed.

Small plants of sweet peas inoculated by bruising the epidermis wilted and developed *Glœosporium* acervuli in about ten days.

Inoculations through punctures on fruits of *Citrus* sp. produced a sort of a wet rot in about a week. *Glœosporium* acervuli were developed in the brown rotting tissues.

Inoculations on onions (*Allium* sp.), sugarcane and jowar leaves, mango fruits, pods of *Phaseolus vulgaris*, have been unsuccessful.

Anthracnose of Carica papaya.

On this host the disease is to be found on flowers, fruits and flower-stalks. It has not been observed on leaves and on living stems at Pusa, though *Colletotrichum* sp.[1] has been recorded on leaves and stems, and also on fruits in Barbados.

Diseased flower-buds do not open but turn brown, become dry and soon fall off. The diseased parts are punctuated by small dots which are at first pink in colour but later they turn black or brown. If the infection takes place when the floral whorls have opened, the diseased floral leaves turn brown and wither. From these leaves the disease may travel to the base of the ovary and to the flower-stalk.

The most critical period when the fruits get infected is when they are newly set, when the pale whitish yellow colour is still persistent and when they are not in latex. A considerable amount of damage is also done to the fruit after it has turned distinctly green and after the laticiferous tissues are developed. Such fruits are generally infected when they are not more than about two inches in length. Bigger unripe fruits are very seldom infected. Fruits that have begun to turn yellow and ripe at times get diseased. But the percentage of the loss of big fruits is negligible.

---

[1] *Agricultural News*, XIV, No. 341, p. 174, 1915.

The infection of the newly set and young green fruits takes place generally either through the stigmas or through the scars left by the floral leaves. If the infection starts from the stigmas the fruit shows a pinched-in appearance. If it starts from the scars left by the fallen floral leaves the base of the fruit becomes sunken and the depression runs into folds and the fruit generally becomes flattened out. The infection can also take place through punctures on the skin. Where there is the infection there appears a circular saucer-shaped depression in the skin. This depression increases concentrically with the progress of the disease. The fruit ultimately completely loses its normal shape. The diseased young fruit loses its green colour and becomes pale yellow, green or white yellow. From the centre of the diseased spots latex exudes in tiny drops. On the newly set fruit, which is still whitish yellow in colour, the infection may also start through its uninjured walls where the presence of the disease is marked by a circular depression which increases in diameter along with the growth of the fungus. If fruits which are about to ripen become diseased, it has been found as a rule that the infection starts from several points which are visible in the early stage as round water-soaked depressions. These diseased areas do not merge into each other but get delimited by a ridge being formed between the neighbouring depressions. In rare cases a single infection spreads over the whole fruit. The diseased area grows concentrically; the old infected tissues are thrown off in dry flakes.

The diseased fruit, especially the very young fruit, becomes mummified, hard and woody, and soon loses its normal shape. If the fruit is cut through a diseased spot the infected tissues are sharply demarcated from the healthy tissue. The diseased part in section is crescent-shaped, dry and pale white in colour which is very conspicuous if the fruit be ripe. The white diseased sunken tissues can be lifted off with a pointed instrument.

The diseased areas when fresh are generally found to be fleshy pink in colour and moist, due to the presence of innumerable acervuli. The acervuli on drying either remain pink coloured or turn black from margin inwards. Till lately, the acervuli were found without setae. But diseased fruits examined in 1917 have shown the presence of setae. Diseased spots with and without setae are as a rule distinct from each other and the former are distinguished from the latter by their black and bristly appearance; but in some cases acervuli with setae have been observed to have developed on incubation in diseased spots which had formerly acervuli without setae. The same has been observed in the case of the acervuli of the *Glomerella* on chillies. On only two or three occasions has the perfect form been found on the fruit. This form has been observed to develop in the old diseased spots in which were formerly the acervuli. The pink colour of the acervuli without setae is lost by degrees and changes into black as dark brown coloured hyphae begin to develop from margin inwards. Ultimately the concentric arrangement of the acervuli in the diseased spot is lost and the once round and sunken spot becomes covered by an undulating rugged and carbonaceous crust. The gradual change due to the development of the perithecia is not so well marked in the spots having acervuli with setae on account of the black colour. The formation of the perithecial stage becomes noticeable by the presence of the undulating rugged crust.

Fruit stalks.

The disease extends to the fruit stalk from the infected fruit but in a few cases the infection has been observed to originate from the stalk. The diseased stalk becomes dry and hard as does the diseased fruit. These dry stalks with the dead fruits remain hanging on the tree for a long time after they are mummified. So far, the acervuli on the stalks have been found without setae. They are not crowded together or confined to a definite area as on the fruit but they are scattered.

Sections through a diseased spot show that in the development of an acervulus there is at first in the epidermal and subepidermal cells a collection of hyphae which form a distinct stroma of pseudo-parenchymatous cells before conidiophores are developed as in the case of chilli *Glœosporium*. This stroma is at first hyaline but later turns brown from the margin inwards. The stromatic cells are uninucleate. Conidiophores are developed from the uppermost cells of the stroma. They are hyaline and broad at the base but tapering at the end (Fig. 9). From the tips of the conidiophores uninucleate elliptical and hyaline spores are cut off in succession. If sections are made through a diseased portion bearing the perfect stage, perithecia are found seated on or partly immersed in a stroma of loosely interwoven brown hyphae. The neck is usually very distinct but this part of the perithecium is very variable in size. At times it is markedly hairy, as hairy as the perithecia of the chilli *Glomerella* figured by Miss Stoneman; in some cases the neck is slightly tufted, while in others it is untufted. The perithecia are flask-shaped, caespitose, membraneous and dark brown in colour. They measure 315·7–385 ×123·2–292·6μ.

The asci (Figs. 10, 11 and 12) are sessile and clavate and measure 60·0–93·5 × 88–12·1μ.

The ascospores (Fig. 13) are hyaline, slightly curved, subdistichous and elliptical. They measure 13·2–20·9 × 4·4–6·6μ. In old perithecia the ascus wall has been found to be disintegrated, setting free the ascospores. In these old perithecia the ascospores are found to be empty of their protoplasmic contents and to have become septate, generally once and rarely twice, and their walls have turned distinctly pale brown in colour, as in the case of the chilli *Glomerella*.

The perfect stage of the *Carica* anthracnose is identical with the chilli *Glomerella* in both morphological and cultural characteristics.

SUMMARY.

Glœosporium piperatum E. and E. and *Colletotrichum nigrum* E. and Hals. are not known to be destructive to chillies in India but they cause much loss of fruit in Burma.

These fungi are considered to be identical and to be the conidial forms of *Glomerella cingulata* (Stoneman) Spauld. and v. Sch., which is shown to be synonymous with *Gnomoniopsis* (*Glomerella*) *piperata* Stoneman, the ascogenous stage of *G. piperatum* E. and E., according to Miss Stoneman.

The perithecia-producing faculty does not depend on the nutrient medium on which the fungus is grown but depends on the race or strain.

This faculty is not a fixed hereditary character but is lost by cultivating successive generations on the same medium at room temperature.

There is a great deal of variation in the size and hairiness of the neck of the perithecium and in the size and shape of asci, and therefore cultural characteristics cannot be much relied upon for determining the species.

The perithecia are aparaphysate.

The ascospores are hyaline, unicellular and slightly curved, but in old perithecia they are found to be septate and their walls coloured brown.

In cultures the presence of setae is not a constant character.

In cultures of the perithecial strain there are very often sudden variations in the characters of the growth of the fungus.

It is doubtful if inoculation experiments are of much value in establishing the relationship of the *Glomerella* on chillies with the other species of this genus or in finding its range of hosts, as the success of inoculation depends on several factors all of which may not be controllable.

Inoculations on chillies, *Carica papaya*, and other plants have been described.

A new disease of *Carica papaya* is described. It is caused by the conidial forms of a *Glomerella*, which is identical with that on chillies in both morphological and cultural characteristics.

The disease is found on flowers, young fruits and fruit stalks. Diseased flower-buds do not open but fall off. If the infection takes place when the flower whorls have opened they turn brown and wither.

The most critical period when the fruits get infected is when they are newly set. Older fruits also at times get diseased.

Newly set and young fruits get the infection through their stigmas or through the scars of the floral leaves or through punctures on the skin.

The infection is marked by the presence of a circular saucer-shaped depression in the skin.

Diseased fruits become mummified, hard and woody.

The study of the conidial forms of the *Glomerella* on *Carica papaya* also shows that *Glœosporium* and *Colletotrichum* are one and the same fungus.

EXPLANATION OF PLATE X

Figs. 1 to 8. *Glœosporium piperatum* on chillies and its perfect stage *Glomerella cingulata.*

Fig. 1. Transverse section of a chilli fruit showing the penetration of the germ-tubes from appressoria. × 421.

Fig. 2. Acervulus of *Glœosporium* on a chilli fruit. × 256.

Fig. 3. Germination of conidia. × 418.

Fig. 4. Perithecia of *Glomerella piperata.* × 88.

Figs. 5 and 6. Asci showing variation in size. × 418. Fig. 5 (*a*) a group of asci from a culture, *b* and *c* asci from the host. Fig. 6, asci from inoculated chilli seedlings.

Figs. 7 and 8. Ascospores, × 418, and their germination × 53.

Figs. 9 to 13. *Glomerella cingulata* on *Carica papaya.*

Fig. 9. Acervulus on a *Carica* fruit showing uninucleate cells. × 553.

Figs. 10 and 11. Asci from culture. × 418.

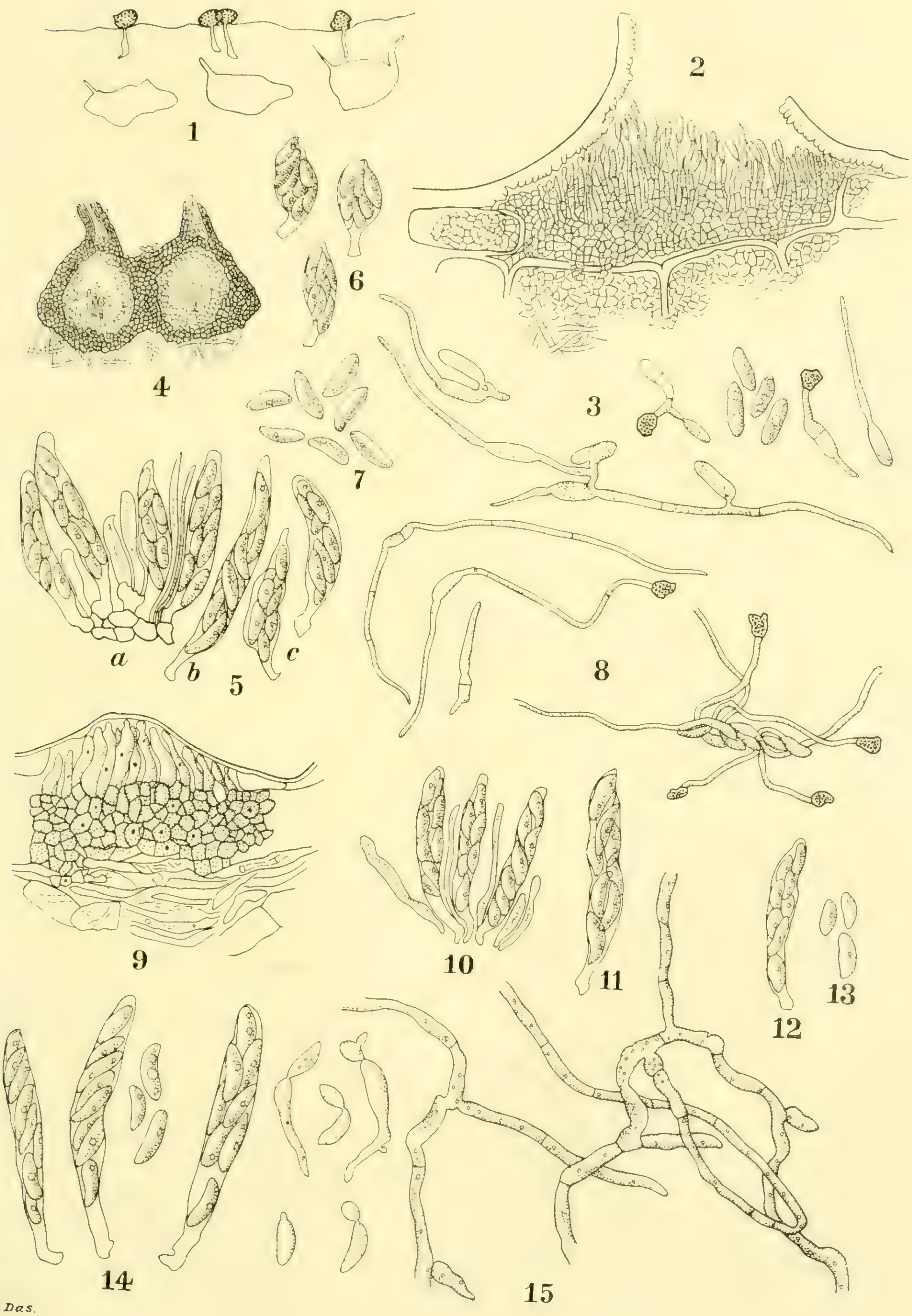
Fig. 12. Asci from a *Carica* fruit. × 418.

Fig. 13. Ascospores. × 418.

Figs. 14 and 15. *Glomerella cingulata* the perfect stage of *Colletotrichum nigrum* on chillies.

Fig. 14. Asci and ascospores. × 418.

Fig. 15. Germination of ascospores. × 418.


1
2
6
4
3
7
a
b
c
5
8
9
10
11
12
13
14
15

K. D. Das.

FIELD EXPERIMENTS ON THE CHEMOTROPIC RESPONSES OF INSECTS.

By A. D. IMMS, M.A., D.Sc.,

Chief Entomologist, Institute of Plant Pathology,
Rothamsted Experimental Station, Harpenden;

AND

M. A. HUSAIN, B.A.,

Government Entomologist, Agricultural College, Lyallpur, Punjab.

(With 1 Text-figure.)

PART I.

PRELIMINARY EXPERIMENTS.

CONTENTS.

		PAGE
I.	Introductory Remarks	269
II.	General and Historical	271
III.	Methods	277
IV.	Observations conducted at Lymm (Cheshire) ...	282
V.	Bibliography	291

I. Introductory Remarks.

A survey of the literature of applied entomology brings home the fact that the efforts of economic entomologists have been largely confined to the discovery of the means of destroying injurious insects; to studying their life-histories, and to ascertaining the most vulnerable stage thereof for the application of remedial measures. During the last few years artificial means for the destruction of noxious insects have progressed rapidly, and even the comparatively recent methods of combating them by the agencies of parasites have made remarkable advances. In all that has been achieved, however, it is evident that the scientific aspects of investigation have constantly been sacrificed in the interests of results derived by empirical methods. Insecticides are used throughout the world and yet we scarcely possess any knowledge as to how they act. Since 1787, when the Abbe Roberjot first discovered the method of destroying the vine moth (*Sparganothis pilleriana*) by means of light, the application of this method has developed rapidly, and there are now in existence ingenious traps, elaborate lanterns and even expensive and complicated electric installations; but strange as it may seem, it was not until 1904 that the study of the effects of light of different colours, in attracting insects, was first taken up by Perraud. Even to this day our knowledge of the physical side of the subject is far from adequate; much research is also needed with regard to the influence of meteorological conditions, and we know comparatively little concerning the proportion of the sexes of the insects attracted. Chemotropism has shared no better fate, and we are largely in the dark as to the influence of the various constituents of those baits extensively used by economic entomologists. Molasses forms one of the most important ingredients, but we are totally ignorant as to which constituent (or constituents) of this complex substance exercises chemotropic properties. Dewitz (1912), Tragardh (1913) and Imms (1914) have emphasised the need for physiological research in applied entomology, but such research they insist must be carried on with a broader outlook than that of modern applied entomologists. The possibilities that the investigation of chemotropism offers, both as regards the application of results achieved and the advancement of scientific knowledge, can be well appreciated by reference to the work of Verschaffelt (1910), Howlett (1912, 1914, 1915), Barrows (1907), Richardson (1916, 1917) and others. There is hardly any doubt that one of the most promising aspects of applied entomology lies along these lines and, as will be pointed out on a later page, in chemotropism we should seek for new and effective measures for combating insect enemies. The control of the house-fly supports this contention, but we are only at the threshold of an extensive line of investigation.

The present paper only embodies observations of an essentially preliminary nature and were carried out by M. A. Husain at the suggestion of the senior author (A. D. Imms); the interpretation of the results and the writing of this article is a conjoint production. Delay has been inevitable in the preparation of this paper owing to one author being transferred to India, while the other was located at the Rothamsted Experimental Station, Harpenden. The necessary laboratory work was conducted in the Department of Agricultural Entomology, Manchester University. We are greatly indebted to Messrs C. G. Lamb, P. H. Grimshaw and H. Bury for help in identifying numerous specimens of Diptera.

II. GENERAL AND HISTORICAL.

Chemotropism is the response of an organism to the stimulus of chemical substances manifested, if the stimulus be responded to, in movements towards (positive chemotropism) or away (negative chemotropism) from the source of stimulus. Dewitz (1912) was the first to emphasise the importance of the study of tropisms in relation to applied entomology and dealt largely with phototropism. Tragardh (1913) laid stress upon chemotropism and pointed out possibilities of its application in combating destructive insects. There is no doubt that various tropisms play a vital part in the economy of insect life but, of these, chemotropism is the great controlling factor. The phenomenon is particularly evident in the search for food, in the pursuit of the sexes and the selection of suitable breeding places: it is also evident in many *apparently* unpurposeful responses. As Loeb remarks (1918), the Aristotelian point of view still prevails in biology namely, that an animal only moves for a purpose, either in connection with those functions just enumerated, or in relation to something else connected with the preservation of the individual or the race. In the words of this writer, "Science began when Galileo overthrew the Aristotelian mode of thought and introduced the method of quantitative experiments which leads to mathematical laws free from the metaphysical conception of purpose. The analysis of animal conduct only becomes scientific in so far as it drops the question of purpose and reduces the reactions of animals to quantitative laws." While admitting the justice of Loeb's remarks, we do not consider it desirable to eliminate all question of purpose from work of this nature, as the habits of a particular species not infrequently suggest the application of substances of chemotropic value, improbable to come under notice, except fortuitously, in other ways. Nevertheless, in many instances, it is remarkably difficult to prove that the observed facts bear the relation to a particular function which at first sight appears evident. The use of baits to attract insects was known to agriculturists of a hundred years ago, and when our forefathers found their land to be infested by wire worms they adopted the plan of burying beneath the soil slices of potatoes impaled on skewers (Weiss, 1912). These were examined frequently and the larvae which were attracted were collected and destroyed. One of the first important contributions to the scientific study of chemotropism, with reference to insects, is the work of Barrows (1907) who investigated the reactions of the pomace fly to odorous substances. This insect occurs in great numbers around cider-presses, packing sheds, orchards and other situations where fermenting fruit is present; within the latter it deposits its eggs and its larvae develop. Barrows investigated the reactions of this fly to the various chemical constituents of fermenting fruit. Ethyl alcohol, acetic ether and acetic and lactic acids were experimented with separately, and in mixture. The insect was found to be attracted in the most marked degree by a mixture of ethyl alcohol of 20 per cent. strength and acetic acid of 5 per cent. It was further discovered that cider vinegar and fermented cider contain alcohol and acetic acid in percentages very close to those just quoted. A series of experiments were conducted proving that the fly discovers its food by means of the olfactory sense, the latter being located in the terminal joint of the antennae. In 1908, Forbes experimented with various reagents with reference to the Corn Root Aphis, with the object of discovering substances towards which this species reacts negatively. The seeds were treated with various chemicals of which carbolic acid, formalin, kerosene and oil of lemon were found to be of value as repellants, aphis attacks being noticeably reduced after the seeds had been thus dealt with. In 1910 Verschaffelt published an important and highly suggestive paper, embodying his investigations of the factors which determine the selection of food in the case of the larvae of *Pieris brassicae* and *P. rapae*. The larvae select as their food plants certain Cruciferae, also *Tropaeolium* and *Reseda*. In these plants there occurs a group of glucosides—the mustard oils. Verschaffelt took a solution of sinigrin, which constitutes the glucose agent in black mustard, and uniformly distributed it over the leaves of plants which the *Pieris* larvae had previously refused to eat. Leaves so treated were devoured readily. From such experiments it appears that the *Pieris* larvae exhibit a marked chemotropism towards mustard oils, and it is due to their presence in the leaves of certain plants that determines the selection of the latter by the larvae for their food. By a similar method of research, Verschaffelt has shown that the larvae of the saw-fly, *Priophorus* (*Cladius*) *padi*, which feed on certain of the Rosaceae, are attracted by the glucoside known as amygdaline. As regards those factors which determine the females to select certain species of plants for purposes of oviposition, definite information might be acquired by carrying out an analogous series of experiments. In 1911 Patterson observed that flies (Sarchophagidae) would not oviposit on freshly killed material (caterpillars) in the cages even though the females had been ovipositing previously on older decomposing caterpillars. This would tend to show that the material must reach a certain stage of decomposition before the female would oviposit. In 1912 Howlett published some observations dealing with the reactions of certain Indian fruit flies. He found that citronella oil exercises a remarkable attraction for the males of *Dacus diversus* and *D. zonatus*, and suggested that possibly this reagent is allied to a secretion emitted by the females, and that the phenomenon of the only being attracted is to be regarded as a reproduction, by artificial means, of a sexual attraction similar in kind to that which operates in most cases of "assembling." In a later paper (1915), Howlett conducted a further series of experiments, confirming his previous results that certain odours are remarkably attractive to male flies of the genus *Dacus* and, that by the employment of attractive substances, the movements of the flies can to a great extent be controlled in any given direction. Three of the common species (*D. diversus*, *ferrugineus* and *zonatus*) normally breed respectively in (1) anthers of Cucurbitaceae, (2) fruits of Solanaceae and mango, and (3) peach, guava, mango and other fruits. *D. diversus* (1) is most strongly attracted by iso-eugenol, *zonatus* by methyl-eugenol, and *ferrugineus* (2) by both iso- and methyl-eugenol. The odours of these substances have not yet been identified with those of the plants which constitute the normal breeding-places, but male flies have been found attracted to mango, Papaya, a Cycad and *Colocasia*, plants with a very characteristic smell similar to that of eugenol-derivatives. Females have never been seen to frequent these plants or to breed in them, but more extended observation on this point is needed. Three explanations suggest themselves. (*a*) That the smell is a direct sexual guiding smell, emitted by the female as previously suggested, but the young crushed females do not attract males. (*b*) The smell is not emitted by the female, but may be termed an "indirect" sexual guide to the plants where the females are accustomed to congregate for breeding purposes. Under these circumstances it is difficult to see why females should not be attracted by the odoriferous chemicals. (*c*) The odour is a food smell; if this be so it can only be attractive to males. It is evident that further critical research is greatly needed eliminating, at any rate for the time being, the metaphysical conception of purpose. In a third paper Howlett (1914) noted the marked response of Thrips to the stimulus of the odours of benzaldehyde, cinnamylaldehyde and anisaldehyde. In his earlier paper (1912), Howlett conducted a further series of experiments with regard to the influence of reagents upon oviposition and it appears not unlikely that the odours of chemical substances provide the required stimulus. Thus, he found *Sarcophaga* to be very strongly attracted to a flask containing a solution of skatol, a substance normally present in faeces and many larvae were deposited therein. *Stomoxys calcitrans* was also induced to oviposit on cotton wool soaked with valerianic acid—a substance occurring in decaying vegetable refuse. Howlett further adds that both valerianic and butyric acids have a similar attraction for an Ortalid fly of the genus *Ulidia* (?) in India. H. H. P. and H. C. Severin (1913–15, 1918) have made a series of studies on the attraction of kerosene for the Mediterranean fruit fly, *Ceratitis capitata*. Enormous numbers of this species have been trapped by the agency of kerosene in various parts of the world, but the number of females attracted is negligible. This species is also attracted by crude petroleum, naphtha distillate, gasolene, etc., all mineral oils that do not normally occur in the environment of the species. Chatterjee (1915) in India has discovered that kusum oil (oil from *Schleicheria trijuga*) has a marked attraction for both sexes of the Coreid bug *Serinetha augur* Fabr., and also for the nymphs in all stages. Dean (1915) has discussed the value of poisoned bran mash flavoured with orange or lemon juice and distributed over areas infested with grasshoppers, army worms, cut worms, etc. In each case the chemotropic value of the mixture was greatly enhanced by the addition of orange or lemon. According to Simpson (1918) tsetse flies are attracted by oil of cloves, essence of orange and essence of lemon. In Queensland, Jarvis (1916) has found that the cane beetle (*Lepidiota albohirta*) is not influenced by the oils of plants allied to its food plant, but is attracted by cajeput oil, acetic acid, carbolic acid, nitrobenzene, and especially oil of almonds. We have, therefore, numerous instances of responses towards substances which do not occur in the normal surroundings of an insect.

The chemotropic responses of the house-fly have been more extensively investigated than those of any other insect. Thus Morrill in 1914 conducted a series of experiments with a variety of substances some of them of great chemical complexity, and varying very much in their chemotropic properties. Among others vinegar and beer (under certain conditions) were both found to be markedly attractive; formalin varied exceedingly. Commercial alcohol (95 per cent.) 1 pint, and water 20 pints, was found to be more attractive after the addition of sugar. The addition of bread to alcohol and alcohol mixtures increased their attractive properties, and also those of various other substances. Commercial dried blood, moistened with water, was found to have an attractive value greater than fresh and decomposed meat and fish. Cane syrup, and sugar and water, were found to have relatively low attractive values when used without other materials. Buck (1915) conducted somewhat similar experiments and found that not less than 3 per cent. nor more than 8 per cent. of 95 per cent. ethyl alcohol in water was a good attractive agent. Sucrose was found to be a valuable addition to various baits, sometimes increasing their attractive properties 10–20 per cent. According to Richardson (1916) the female house-fly is strongly attracted towards manure for purposes of oviposition, food being only a secondary object. He exposed a number of liquids and found that ammonium carbonate was the most attractive. Small amounts of water and carbon dioxide, both constituents of ammonium carbonate, were not sought after by the flies, and it was concluded that the other constituent, ammonia, was the real attracting agent. Of the flies attracted only 7·6 per cent. were males. His experiments indicated that manure which was liberating ammonia was more attractive than fresh manure. Richardson was successful in inducing oviposition on a mixture of moist Timothy chaff and ammonium carbonate, whereas the chaff alone produced no result. In experiments conducted with moist sterilised absorbent cotton, ammonium carbonate exercised practically no chemotropic stimulus for oviposition, but was effective when traces of butyric acid were added: valerianic acid was attractive to a lesser degree. Crumb and Lyon (1917) investigated the question more fully, and produced evidence suggesting that carbon dioxide is the chief stimulant for oviposition, giving an 82 per cent. higher stimulus than ammonia. Richardson (1916) conducted some further experiments with reference to the attraction of Diptera to ammonia and found that it attracted various species. Those which respond to this stimulus are known to spend at least part of their lives in some form of animal excrement. The response is not always a simple one as was shown in his earlier investigation. In this same paper Richardson remarks that he was unable to induce *Stomoxys calcitrans* to oviposit on cotton wool soaked in valerianic acid, although Howlett was successful with this experiment in India. In 1917 Richardson conducted a series of tests with reference to the house-fly, using a wide range of substances placed in fly traps. A number of carbohydrates were tested in solution and, on the whole, they did not prove very attractive: lactose attracted the largest number of flies and starch the least. Dextrin also caught a comparatively large number of flies, but sucrose was consistently a poor attractive agent. In using alcohols and acids he found that 4 per cent. amylic alcohol gave better results than ethyl alcohol. Ethyl alcohol in 4 per cent. strength was more attractive than in 10 per cent. concentration; 10 per cent. acetic acid gave better results than 4 per cent. Succinic and lactic acids exhibited some attractive qualities in two experiments. Maltose, lactose, sucrose and dextrin in 4 per cent. solutions of amylic alcohol, ethyl alcohol and acetic acid were found more attractive than the aqueous solutions of these substances. Crude gluten from wheat flour was not attractive. The water soluble portion, with or without starch in suspension, was decidedly attractive. Several experiments with milk indicated that fat-free caseinogen is attractive while butter fat is not. In 1918 Miss Lodge published a paper on the sense-reactions of flies—mainly those species likely to be concerned with the spread of intestinal diseases. The experiments were conducted indoors, and the different substances were tested both upon free flies and those confined in glass cylinders provided with muslin tops. The authoress states that the most suitable medium for the experimental tests was found to be equal parts of casein, sugar and banana, to which a solution of the substance to be tested was added. In all cases, therefore, an extraordinarily complex chemotropic substance was utilised, to which was added various other chemical agents of varying complexity. The results showed that, although many of the substances attracted a certain number of Diptera present in the room, yet none were so attractive that all the flies went to them. Pyrethrum extract, added to the medium already described, proved very attractive to *Calliphora*, ammonia proved attractive to *Phormia azurea*, ammonia and honey to *Musca domestica*; the latter insect was also attracted by honey and methylene blue, 1 per cent. nicotine, ammonium carbonate, and other substances. The addition of an aqueous solution of skatol was attractive to *Calliphora* and *Scatophaga*; camphor attracted *Calliphora* and also honey, the latter substance was attractive also to *Lucilia caesar*. As a control the casein mixture was adopted and this substance proved more attractive to *Calliphora* and *Lucilia* than any other reagent when added to it. Mineral and tar oils proved to be powerful repellents, the essential oils were, on the whole, repellents. Davidson (1918) states that 12 per cent. glycerine and 5 per cent. sugar to which was added 1 per cent. sodium arsenite proved a successful poisonous attractive agent for flies during the Egyptian campaign of the late war. Parker (1918) found a combination of beer and oatmeal proved a most attractive substance for the females of various Diptera frequenting privy vaults in Montana.

In the foregoing summary of the literature bearing upon Chemotropism we have included the more important papers but it makes no pretence of being exhaustive. A further object of this resume is to emphasise the fact that no systematic quantitative work has yet been attempted, and most of the observations so far recorded concern particular species only. A large number of chemical substances are sufficiently volatile to merit adequate trials, and it is our intention during these researches to examine as many as possible, recording the species which respond, irrespective of whether they are injurious or otherwise. We are of opinion that quantitative work of this kind will provide a broader basis for a scientific understanding of the problems involved, than specialised experiments conducted for the purpose of combating any particular species of injurious insect.

III. METHODS.

Experimental researches upon chemotropism divide themselves into two groups—those conducted under the more or less artificial conditions of an enclosed room, and those carried out under field conditions. It is scarcely necessary to add that preliminary experiments in any branch of physiology need to be carried out under definitely known and controllable conditions of temperature, light, humidity, air currents, etc., and in such a way as to eliminate as many of these factors as may be desired. Such simplified conditions are scarcely possible in researches of the nature under consideration, except in the case of experiments conducted indoors. Our present researches are entirely concerned with field experiments, and we are firmly of the opinion that preliminary indoor trials are of little value in this connection. Insects reared and liberated under artificial conditions, and surrounded by a totally alien environment, do not necessarily react in a manner similar to those living free in their natural habitat. In the case of insects concerned with the spread of disease, and normally frequenting dwellings, hospitals, etc., these remarks naturally do not apply, and their reactions form no part of our observations.

Chemotropic work in the field presents innumerable difficulties and in no line of biological research with which we are acquainted is there so large a number of environmental and other factors to be taken into consideration. Success or failure of any chemotropic experiment depends primarily upon the presence of favourable atmospheric conditions. One is therefore largely at the mercy of climatic influences, which, in a country like England, are extremely variable. Temperature, air-currents, humidity, etc. have a direct bearing upon the evaporation of the substances to be tested, and the dissemination of their odours. Furthermore, atmospheric changes influence the tropisms of insects to a marked degree. Degree of temperature and amount of sunshine affect their activities, a dull cloudy day may inhibit their movements very noticeably, a strong wind interferes with flight, and excess of moisture inhibits their activities in other directions. There are also many unknown factors which exercise their influence in different ways: the time of day, season, degree of development of the gonads, age of the insects concerned, state of hunger, development of the eggs, whether oviposition is in progress or not, all probably have a definite bearing upon the chemotropic responses of insects, but we are totally in the dark as to how they manifest themselves. We have observed, and also Richardson (1917), that the same attractive substance may vary in effectiveness on different days under apparently similar atmospheric conditions. This may be due to one or other of the above-mentioned factors, or depend upon the actual number of insects present in a given locality at a particular time, or may in some way be correlated with sex attraction. Feytaud in his experiments in trapping moths discovered that some traps lured exceptionally large numbers, especially at the end of the season, and in some cases in the proportion of only two females to 54 males. He attributes this to sex attraction, females being trapped first, males subsequently following them. In view of the complexity of the factors which have to be taken into account, it is necessary to repeat every individual experiment a number of times during the season, and keep very full meteorological data. It will consequently be evident that reliable results, concerning the chemotropic properties of even a small number of substances, take several years to achieve.

All experiments to have any scientific value must be checked by a definite control. When a chemical agent is exposed, and it attracts certain insects, we acquire definite data. The question then to be gone into is its relative attractive value as compared with other substances. To prove that any substance exhibits attractive properties we are faced with a number of problems. The negative results do not necessarily imply that the agent has no attractive value, as the species which may respond to the stimulus may be absent from the immediate locality at a given time. It is, therefore, necessary to devise a double control—one to prove that certain species of insects are actually present at the place and time of observation, and the other to show that the substance being dealt with has, or has not, chemotropic properties. As mentioned above, water may serve as one control, but to devise the second control substance is less easy of achievement. It is necessary to use a substance known to exhibit powerful chemotropic properties and this, in itself, is liable to vitiate the experiment in attracting insects which might have otherwise responded to the substance required to be tested. The senses of insects are very acute, and minute traces of a reagent are known to produce marked results. We are also totally ignorant as to the distance which the odour of a particular substance may exercise chemotropic properties. According to Howlett (1915) the radius of attraction of citronella oil for certain fruit flies may be taken as about half a mile: with many Lepidoptera the female probably attracts the male from a much greater distance. It is evident, therefore, we should guard against placing substances to be tested too near to each other. For every agent to be tested suitable controls have to be decided upon, and spaced as far apart as may be possible.

In our field experiments we have to obtain the following data:

(1) Power of attraction of a substance in various dilutions and under varied atmospheric conditions.

(2) Optimum attractive strength.

(3) Relative powers of attraction as compared with other substances.

(4) The species attracted, their numbers and the proportion of the sexes.

(5) Meteorological data.

There are two methods of discovering substances likely to exhibit chemotropic attraction. The one is to undertake experiments with any substance that normally occurs in the environment of particular species, *e.g.* a constituent of the food of the larvae or adult, or likely substances chemically allied to the same. The second method is to test a large number of substances, necessarily somewhat indiscriminatingly at first, in the hope of discovering attractive agents. Verschaffelt (1910) observed that the alkaloid that gives mustard oil is the attractive agent in the larval food of *Pieris brassicae*; he started with the food plants and worked with the ingredients thereof. Richardson, who has studied the reactions of the house-fly to various agents, also followed this same method. He first observed that the house-fly is attracted to the manure heap by the odour of certain substances, which were being liberated during the early stages of fermentation. On this basis, he experimented with various inorganic and organic compounds that occur in the manure heap. This method is full of possibilities, in so far as individual species are concerned, but the second of the above methods has its advantages for preliminary quantitative work. It has been observed that a large number of insects are attracted towards chemicals that are neither associated with the smell of their food substances, nor occur in their normal environment. It is, moreover, in the discovery of such substances that some of the most striking results have so far been achieved. We have therefore followed this method of exposing a large number of chemicals and recording the results. So far as possible we have worked with simpler substances, leaving the more complex organic compounds for later work. It is hoped that by this method it will be possible to discover whether any general relationship exists between chemical constitution and attractive properties.

The question of a suitable trap for exposing the agents used is of very great importance. It is essential that the substances to be tested should be exposed in traps so constructed as to admit any insects that are attracted thereto and, at the same time, preclude their escape. A free outlet for the uniform dispersal of the odour of each reagent used is essential and, furthermore, the constructional materials must be inodorous, and must not be readily acted upon by chemicals. Convenience of size and handling should not be overlooked, and the traps should be readily washable whenever necessary. After trials with various types of traps it was found that one based upon the Minnesota model (Washburn, 1912) was more suitable than any other. It possesses, however, the defect that insects can only enter around the base of the trap, and it is extremely likely that a certain number of insects which may be attracted do not succeed in entering. We have mainly used a rectangular trap of this type measuring 11″ × 7″ × 9″ covered with ordinary fine white muslin, which can be readily renewed when necessary. The colour or condition of the trap appears to exercise some influence in the attraction of insects. Thus Dewitz (1912) states that white saucers are more attractive than coloured ones. Morrill (1914) also observed that insects came more readily to a new balloon trap than to a rusty trap. During trials conducted with clean empty traps, however, we found that the number of insects which entered therein was negligible. The greatest number was five Diptera and one Lepidopteron, after 36 hours exposure. In each experiment 50 c.c. of a chemical substance of a known strength was exposed for a given time, and full details recorded of any species attracted. It proved difficult during these preliminary trials to keep full meteorological data but, as far as possible, a record of maximum and minimum temperatures, both by means of ordinary and wet and dry bulb thermometers, was kept and the general conditions of the weather noted.

During one trial an empty trap was exposed on one occasion and we were surprised to find a considerable number of Diptera entrapped. On the previous day this same trap contained a markedly attractive agent and many insects were caught. It appears, therefore, evident that either the odour of the previous reagent lingers, and still exercises chemotropic properties or, possibly, some smell is emitted by the flies themselves and their faeces, and serves to attract further individuals. The importance of using perfectly clean traps is thus rendered particularly important. The traps were suspended from trees and posts at a height of 2–4 feet from the ground. Owing to the junior author (Husain) having at his

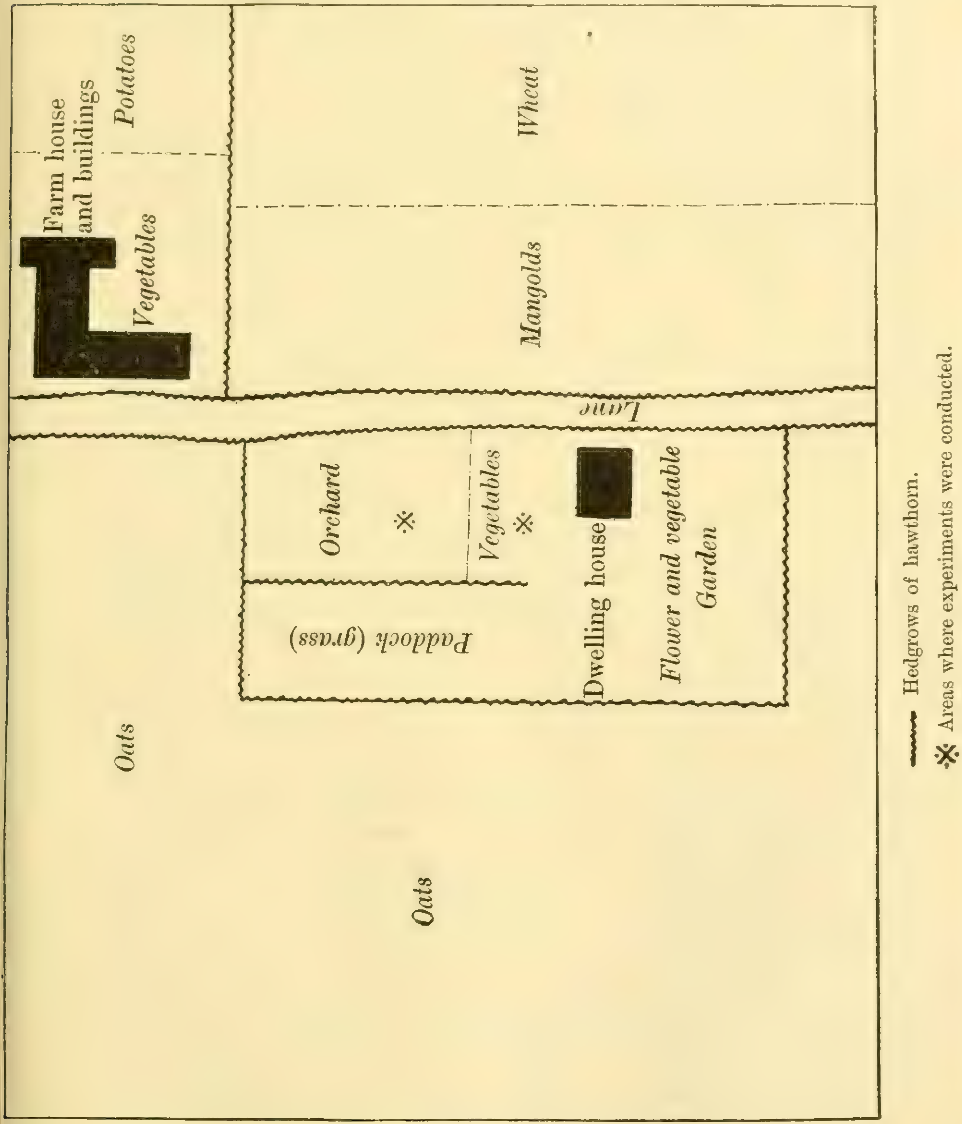

Farm house
and buildings
Potatoes
Vegetables
Wheat
Mangolds
Lane
Orchard
※
Vegetables
※
Dwelling house
Flower and vegetable
Garden
Paddock (grass)
Oats
Oats
Hedgrows of hawthorn.
※ Areas where experiments were conducted.

Fig. A. Somewhat diagrammatic sketch-plan showing the immediate surroundings of the areas where the experiments were conducted.

disposal the short period of only 10 weeks wherein to conduct these experiments, they can only be regarded as essentially preliminary in nature. War conditions also added to the difficulty in procuring certain reagents, and the summer of 1918 proved to be one of the wettest for a number of years. During the months of July–September there was scarcely more than two clear sunny weeks. Our observations were conducted at Lymm (Cheshire) in an orchard and vegetable garden, and the immediate surroundings are indicated in Fig. A. Less than 60 yards away are farm buildings and accompanying manure heaps which provide sustenance for great numbers of Diptera.

The length of exposure of a substance was generally 24–48 hours, but sometimes longer or shorter according to circumstances. Mr Husain, however, has not given very exact data upon this point. In all cases in which long exposures were resorted to, it was owing to adverse weather conditions which necessitated more lengthy trials.

As our observations are the first of their kind conducted in this country, we have deemed it advisable to publish them as they stand, without drawing any definite conclusions therefrom. We have laid particular stress upon the difficulties of the work, with a view of warning other intending observers of the pit-falls they are likely to encounter.

IV. OBSERVATIONS CONDUCTED AT LYMM (CHESHIRE) DURING JULY AND AUGUST, 1918.

(1) The following substances gave negative results, *i.e.* no insects were attracted, and it is probable that some of the agents used are powerful repellents.

	Oil of cajeput		Exposed on two occasions.
	,, orange		
	,, lemon		
	,, sandal wood		
	,, bergamot		
	,, cloves		
	,, juniper		
	Birch tar oil		
	Oil of aniseed		Exposed on three occasions.
	,, citronella		Exposed on six occasions.
	Menthol		Exposed on two occasions.
	Turpeniol		
Aqueous solutions, 50 c.c.	Potassium hydroxide	(5%)	
	Hydrochloric acid	(5%)	
	Sulphuric acid	(5%)	
	Malic acid	(5%)	
	Benzaldehyde	(5%)	

All the oils enumerated above were used both in wire balloon traps and the Minnesota model traps. In one series of experiments a few drops were allowed to fall on blotting paper and placed in the usual receptacle within the traps. In a second series of experiments, an approximately similar quantity of each oil was added to 50 c.c. of water and shaken to form an emulsion.

(2) *Kerosene.* This substance is known abroad to attract insects belonging to such diverse groups as aphids, mosquitos, barklice, moths, cockroaches, Syrphid flies, Coccinellidae and their larvae, also a number of Tachinidae and parasitic Hymenoptera (Severin, H. H. P. and H. C., 1915). In our experiments it was exposed on four occasions: during one exposure it attracted a number of Nematocera, but on the remaining occasions the results were negative. It is important, however, to recognise that the kerosene used in these trials probably differed in composition from that employed in America.

(3) *Vinegar.* The records were as follows:

Aug. 19–30.	40 c.c. vinegar	100 c.c. water	22 Diptera	
Aug. 30–31.	25 c.c. ,,	50 c.c. ,,	3 ,,	
	10 c.c. ,,	50 c.c. ,,	1 ,,	and 1 *Vespa vulgaris*
	5 c.c. ,,	50 c.c. ,,	2 ,,	
Aug. 31.	40 c.c. ,,	100 c.c. ,,	5 ,,	

(4) *Ethyl alcohol.* Ethyl alcohol (approximately 95 per cent. strength) was used in the following percentages, 36, 22·5, 12·5, 10, 7, 5, 3, 2·5, 1, ·7, ·4, and ·2. These solutions (50 c.c.) were used both as controls for other experiments and as independent chemotropic agents, but no attractive properties were evident in any instance. Our experiments with solutions stronger than 36 per cent. were vitiated, and need to be repeated. The 5 per cent. solution attracted eight Diptera and this result was only achieved after 48 hours exposure. Our results are somewhat remarkable in view of the fact that Richardson (1917), in New Jersey, caught 891 examples of *Musca domestica* in the course of six experiments, representing an aggregate of 207 hours exposure, using 4 per cent. ethyl alcohol. This observer found that a 10 per cent. solution, exposed in the same series of experiments, attracted 544 examples of that same species, which made up more than 95 per cent. of the Diptera attracted during the whole course of his trials. The latter were conducted within 50 yards of a prolific breeding ground of the insect, and our own experiments were carried out within 60 yards of farm accumulations of manure, and decaying organic matter of various kinds. Buck (1915), also in America, observed that not less than 3 per cent. and not more than 8 per cent. of 95 per cent. ethyl alcohol was a markedly attractive agent.

(5) *Glacial acetic acid.* Glacial acetic acid was not observed to exercise any marked chemotropic attraction as the following experiments indicate.

Aug. 27–29.	50 c.c. water	5 c.c.	glacial acetic	acid	1 Dipteron
„ 21–23.	„ „	1 c.c.	„	„	Nil
„ 21–22.	„ „	·5 c.c.	„	„	3 Diptera
„ 24–27.	„ „	·5 c.c.	„	„	13 „
„ 27–29.	„ „	·5 c.c.	„	„	12 „
„ 24–27.	„ „	·1 c.c.	„	„	2 „

(6) *Ethyl alcohol* and *glacial acetic acid.* Unlike either of these substances, when used separately, a mixture of the two was found to be markedly attractive. Ethyl alcohol and acetic acid when brought into contact form small quantities of ethyl acetate and, as shown in Barrow's experiments (1907), ethyl acetate exercises a marked attraction for *Drosophila ampelophila.* The amount of ethyl acetate formed by using such small quantities of the two substances as 1 per cent. of ethyl alcohol and 0·05 c.c. of acetic acid under outdoor conditions must be very small. In each experiment 50 c.c. of ethyl alcohol or water was used.

Exp.	1.	Aug. 19–21.	10%	ethyl alcohol	+ 1	c.c.	glacial acetic	acid	69 Diptera
		„ „	10%	„	—	—	—	—	0 (control)
„	2.	„ 21–23.	10%	„	+ 1	c.c.	„	„	329 Diptera
		„ „		water	+ 1	c.c.	„	„	0 (control)
„	3.	„ 21–22.	10%	ethyl alcohol	+ ·5	c.c.	„	„	82 Diptera
		„ „		water	+ ·5	c.c.	„	„	3 „ (control)
„	4.	„ 22–23.	10%	ethyl alcohol	+ ·5	c.c.	„	„	12 Diptera
		„ „	10%	„	—	—	—	—	2 „ (control)
„	5.	„ „	5%	„	+ ·5	c.c.	„	„	41 Diptera
		„ „	5%	„	—	—	—	—	2 „ (control)
„	6.	„ 27–29.	5%	„	+ ·5	c.c.	„	„	214 Diptera
		„ „	5%	„	—	—	—	—	8 „ (control)
„	7.	„ 22–23.	5%	„	+ ·2	c.c.	„	„	14 Diptera
„	8.	„ „	5%	„	+ ·1	c.c.	„	„	7 „
„	9.	„ 23–24.	5%	„	+ ·05	c.c.	„	„	10 „
„	10.	„ „	2·5%	„	+ ·5	c.c.	„	„	25 „
„	11.	„ „	2·5%	„	+ ·1	c.c.	„	„	12 „
„	12.	„ „	2·5%	„	+ ·05	c.c.	„	„	4 „
„	12*a*.	„ „	2·5%	„	—	—	—	—	1 „ (control)
„	13.	„ 24–27.	1%	„	+ ·5	c.c.	„	„	122 Diptera
„	15.	„ „	1%	„	+ ·05	c.c.	„	„	45 „
„	15*a*.	„ „	1%	„	—	—	—	—	0 (control)
„	14.	„ „	1%	„	+ ·1	c.c.	„	„	19 Diptera
„	14*a*.	„ „		water	+ ·1	c.c.	„	„	2 „ (control)

It appears evident, therefore, that the greatest attractive properties are exercised when at least ·5 c.c. acetic acid is present, and they are enhanced by an increased strength of the alcohol. Experiments with greater strengths than 10 per cent. ethyl alcohol were unable to be carried out, owing to adverse weather conditions.

	Experiment nos.															
Totals	2	3	4	6	7	8	9	10	11	12	13	14	15	16	17	
183	123	1	—	18	1	—	—	—	—	—	2	—	—	8	30	*Rhyphus punctatus*
4*	—	—	—	—	—	—	—	—	—	—	—	—	—	2*	2*	
65	42	1	—	7	1	1	—	—	—	—	—	—	—	4	9	
1*	—	1*	—	—	—	—	—	—	—	—	—	—	—	—	—	*Rhyphus fenestralis*
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	
25	7	5	—	4	—	—	—	—	—	—	1	—	1	—	7	*Onesia sepulchralis*
34	4	2	—	4	—	—	—	—	1	—	4	1	—	—	18	
47	11	10	3	3	—	—	1	1	—	—	4	—	1	1	12	*Sarcophaga carnaria*
18	—	4	—	1	—	—	—	1	1	—	2	—	—	1	8	
8	—	—	—	2	—	—	—	—	—	—	1	—	—	1	4	*Pollenia rudis*
1*	—	—	—	—	—	—	—	—	—	—	—	—	1*	—	—	
6	—	—	—	1	—	—	—	—	—	—	1	—	—	—	4	
3	—	—	—	2	—	—	—	—	—	—	—	—	1	—	—	*Graphomyia maculata*
1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	
17	4	2	—	6	1	—	—	—	—	—	—	—	—	—	4	*Muscina stabulans*
10	2	2	—	2	—	—	—	—	—	—	—	—	—	—	4	
5	2	—	—	—	—	—	—	—	—	—	—	—	—	3	—	*Muscina caesia*
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
6	2	1	—	1	—	—	—	—	—	—	—	—	1	—	1	*Muscina pabulorum*
8	4	—	—	2	—	—	—	—	—	—	—	—	—	—	2	
16	—	4	1	5	—	—	1	—	1	1	2	—	—	—	1	*Mesembrina meridiana*
3	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	
71	12	3	—	14	—	—	—	3	1	—	6	1	1	10	20	*Calliphora erythrocephala*
44	6	2	—	14	—	—	3	—	—	—	3	—	1	7	8	
56	9	3	—	17	—	—	—	—	—	—	—	1	3	2	21	*Calliphora vomitoria*
64	7	1	—	16	—	—	—	1	—	—	—	—	3	2	30	
75	19	6	—	16	—	—	—	—	—	—	1	1	2	8	22	*Lucilia* sp.
61	19	3	—	14	—	—	—	—	—	—	2	1	—	4	18	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*Mydaea impuncta*
18	1	2	—	1	—	—	2	2	—	—	3	—	—	2	5	
4	—	—	—	1	—	—	—	—	—	—	—	—	—	—	3	*Spilogaster duplicata*
5	—	—	—	1	—	—	—	—	—	—	—	—	—	—	4	
1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	*Hydrotaea dentipes*
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
110	4	4	1	15	4	—	2	3	—	—	14	3	3	25	32	*Hylemyia strigosa*
243	6	6	5	24	7	4	—	14	7	3	36	9	11	53	58	
2	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	*Hytodesia errans*
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*Anthomyia pluvialis*
2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	
24	6	2	1	2	—	—	—	—	—	—	2	1	—	—	10	*Fannia canalicularis*
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
6	—	1	—	1	—	—	—	—	—	—	1	—	1	1	1	*Scatophaga stercoraria*
5	—	—	—	1	—	—	—	—	—	—	—	—	—	1	3	
208*	34*	14*	2*	17*	—	2*	1*	—	1	—	30*	1*	15*	69*	22*	Unidentified, mostly Anthomyidae
1466	329	82	13	214	14	7	10	25	12	4	121	19	45	204	365	Totals

On Aug. 24–29 (Exp. 17) two vessels were placed closely together in the same trap: one contained 50 c.c. of 5 per cent. ethyl alcohol, and the other 50 c.c. of 1 per cent. glacial acetic acid. The vapours of the two solutions coming in contact would produce very minute quantities of ethyl acetate. This, however, proved to possess powerful attractive properties, 365 Diptera pertaining to various species being entrapped. In another experiment (No. 16) (Aug. 24–27), 50 c.c. 2 per cent. glacial acetic acid was used, and the same quantity of 10 per cent. ethyl alcohol was placed in a second vessel as before, and 204 Diptera were attracted during 42 hours exposure. The question arises whether it is the vapour of the ethyl acetate that is alone responsible for this attraction, or the mixed vapours of the ethyl alcohol, acetic acid and ethyl acetate that produced the effect. This problem is at present unanswered. As a control on the same days (Aug. 27–29) 5 per cent. ethyl alcohol attracted only eight Diptera.

An analysis of the species attracted and the number of each sex obtained is given on p. 285. The numbers at the head of each column refer to those allotted to each of the foregoing experiments. The figures opposite each species refer to the number of individuals attracted, the upper figures representing males and the lower figures females: figures bearing * are cases in which the sexes of the individuals were not determined.

7. *Ethyl acetate.* We have so far only conducted a few experiments with this ester. From Aug. 2–8 an emulsion of 10 c.c. of ethyl acetate in 50 c.c. of water attracted only 39 Diptera. From Aug. 8–12 a mixture of 5 c.c. ethyl acetate and 50 c.c. of a 25 per cent. solution of cane molasses proved attractive. During the same period a trap containing 25 c.c. of beer in place of the ethyl acetate attracted 108 examples of various Diptera.

8. *Methyl acetate.*

Aug. 12–14. 5 c.c. water + 10 c.c. methyl acetate. 3 Diptera.
„ 15–16. 5 c.c. 10% ethyl alcohol + a few drops of methyl-acetate. 11 Diptera.

9. *Amylic acetate.* On Aug. 16–19 an emulsion consisting of 33 per cent. amylic acetate in water attracted seven Diptera: with 20 per cent. amylic acetate six Diptera were attracted, and with 9 per cent. acetate 10 Diptera responded.

(10) *Butyric and valerianic acids.* Normal butyric acid in water exhibited no attractive properties, but traces of this substance in ethyl alcohol proved very attractive, this property probably being due to the ethyl butyrate formed. Iso-butyric acid gave less satisfactory results.

Traces of valerianic acid in ethyl alcohol is also an attractive mixture. The experiments were as follows:

1.	Aug. 15–16.	10% ethyl alcohol	+ traces of butyric acid	39 Diptera
	„ 16–19.	Water	+ „ „	3 „
2.	„ 21–22.	10% ethyl alcohol	+·5 c.c. butyric acid	82 „
	„ „	Water	+·5 c.c. „	2 „
3.	„ 22–24.	10% ethyl alcohol	+·5 c.c. „	20 „
4.	„ „	10% „	+·5 c.c. iso-butyric acid	7 „
	„ „	10% „	— — —	2 „
5.	„ 15–16.	10% „	+ traces of valerianic acid	37 „

The species attracted were as follows: an * indicates that the sex was undetermined.

Exp. 1	Exp. 2	Exp. 5	Species attracted
1♂	2♂	—	*Sarcophaga carnaria*
—	1♀	—	*Pollenia rudis*
1♂	—	—	*Musca domestica*
1♂	2♂	—	*Calliphora erythrocephala*
1♀	—	—	
—	3♂	—	*C. vomitoria*
—	—	1♂	*Mesembrina meridiana*
3♀	2♀	1♀	*Mydaea impuncta*
—	—	1♀	*Spilogaster duplicata*
1♀	2♀	—	*Muscina stabulans*
—	1♂	—	*M. caesia*
—	1♀	—	
—	—	1♂	*M. pascuorum*
—	1♀	—	
10♂	—	5♂	*Hylemyia strigosa*
13♀	2♀	8♀	
4♂	1♂	1♂	*Fannia canalicularis*
4*	64*	19*	Unidentified, mostly Anthomyidae
39	82	37	Totals

(11) *Beer.* Beer has long been known to exercise marked chemotropic properties. It forms an important constituent of a number of baits used on a practical scale, for the purpose of attracting and trapping injurious Lepidoptera. Our observations confirm the high attractive properties of this substance, and we have also been able to definitely prove that it is equally, or even more, attractive in so far as Diptera are concerned. Beer is a complex chemical substance, whose composition varies in almost every sample, and it is essential to ascertain which constituent or constituents exercises this power. Our researches are now being conducted with this object in view.

The following experiments were performed for the purpose of testing the relative value of 50 per cent. solutions of beer and a mixture of beer and cane molasses—the latter itself being an important attractive agent. Two small American balloon traps were fitted up for the purpose and were suspended close together from the same tree. The one trap A was charged with 60 c.c. beer solution and the other trap B was charged with 30 c.c. undiluted beer and 30 c.c. of a 25 per cent. solution of cane molasses, with the following results. July 13–14. Trap A, 11 flies; B, 11 flies. July 14–16. A, 4 flies; B, 57 flies. July 16–19. A, 5 flies; B, 65 flies. It was observed that Diptera responded much more quickly to the stimulus of beer, but the latter speedily lost its attractive properties. After the second day, probably on account of the fermentation which was going on in the molasses mixture, trap B became far more attractive. On July 6–8, 200 c.c. of a 50 per cent. solution of beer in a Minnesota trap attracted 928 Diptera, the largest number recorded in any of our experiments. On July 11–13 a 33 per cent. solution of beer attracted 175 Diptera. The species attracted are recorded below, the figures in brackets referring to the weaker solution. *Scatopse* sp. 11*. *Rhyphus punctatus* Fab. 98♂, 60♀, 27* (5♂, 2♀). *R. fenestralis* Scop. 2♀. *Onesia sepulchralis* L. 20♂, 12♀ (4♂, 6♀). *Sarcophaga carnaria* L. 2♂, 6♀ (5♂, 1♀). *Pollenia rudis* Fab. 8♂ (2♂, 5♀). *Muscina stabulans* Fall. 1♂. *Morellia hortorum* Fall. 1♂, 1♀. *Mesembrina meridiana* L. 8♂, 3♀ (2♂). *Pyrellia eriopthalma* Macq. 8♂, 10♀ (1♀). *Calliphora erythrocephala* Mg. 29♂, 24♀ (3♂). *C. vomitoria* L. 6♂, 3♀ (1♀). *Euphoria* sp. 1♀. *Lucilia* sp. 12♂, 8♀. *Mydaea meditabunda* F. 4♂, 1♀ (1♂, 2♀). *M. impuncta* Fall. 23♂, 11♀ (6♂). *Spilogaster duplicata* Mg. 3♀. *S. pubescens* Stein. 3♂. *S. demigrans* Ztt. (1♂). *Hydrotaea dentipes* Fab. 7♂, 1♀ (1*). *Hylemyia strigosa* Fab. 92♂, 30♀ (37♂, 44♀). *Polietes lardaria* Fab. 3♂, 8♀ (1♂). *Hylodesia marmorata* Ztt. 2♀. *Anthomyia pluvialis* L. 1♀. *Fannia canalicularis* L. 7♂ (2♂). *F. manicata* Mg. 1♂. *Fannia* sp. 17♂, 5*. *Scatophaga stercoraria* L. 16♂, 2♀ (5♂, 10♀). *Themira putris* L. 1♂. *T. minor* Hal. 1♂, 7♀. *Drosophila obscura* Fall. 2*. *Dolichopus griseipennis* Stan., *Piophila vulgaris*, *P. nigriceps* Mg., a few examples of each were attracted by the 50 per cent. solution and many examples of a species of *Sciara* and *Sepsis*. *Helomyza* sp., a few examples were attracted by both solutions. Unidentified Diptera (mostly Anthomyidae) 300 (32).

(12) *Cane molasses.* The variety used was that commonly known as "black treacle"—an extremely complex substance of variable chemical composition. Our researches have not so far included an investigation of the attractive agents present, but it is intended to pursue this line of research at the earliest opportunity. Cane molasses (50 c.c.) was used

in 25 per cent. and 50 per cent. solutions in distilled water, both alone, and with the addition of certain other substances as detailed below.

July 4– 5.	50% solution	... ...	256	Diptera
„ 8–12.	25% „	... ...	36	„
„ „	25% „	+ (50 c.c.) 25 c.c. beer	108	„
„ „	25% „	+ 5 c.c. 10% ammonia	8	„
„ „	25% „	+ 5 c.c. 10% malic acid	12	„
„ „	25% „	+ 5 c.c. 5% acetic acid	4	„
„ „	25% „	+ 5 c.c. ethyl acetate	2	„

It is evident from these results that cane molasses in strong solution is an extremely attractive substance. When used in 25 per cent. solution its chemotropic properties are increased by the addition of beer, but in these experiments the addition of the other substances quoted above had no positive effect.

Species attracted.—50 per cent. solution. *Rhyphus punctatus* Fab. 48♂, 21♀. *Onesia sepulchralis* L. 15♂, 8♀. *Sarcophaga carnaria* L. 2♂. *Pollenia rudis* Fab. 5♂, 4♀. *Muscina* (*Cyrtoneura*) *stabulans* Fall.1♂,1♀. *M. pabulorum* Fall. 3♀. *Morellia hortorum* Fall. 1♂. *Pyrellia eriopthalma* Macq. 1♂, 4♀. *Phormia* sp. 1♂. *Calliphora erythrocephala* Mg. 3♂, 1♀. *Mydaea meditabunda* F. 2♂, 2♀. *M. impuncta* Fall. 11♂. *Spilogaster duplicata* Mg. 5♂. *S. pubescens* Stein. 1♂. *Hydrotaea dentipes* Fab. 2♂, 2♀. *Hylemyia strigosa* Fab. 29♂, 13♀. *Polietes lardaria* Fab. 5♂, 7♀. *Hytodesia errans* Mg. 1♂. *Chortophila trichodactyla* Rond. 1♂. *Fannia* sp. 11♂, 9♀. *Scatophaga stercoraria* L. 2♂, 1♀. *Helomyza* sp., *Themira putris* L., *T. minor* Hal., *Sepsis* sp., *Sciara* sp., a few examples of each Unidentified Diptera, mostly Anthomyidae 30.

25 per cent. solution + 25 c.c. beer.—*Rhyphus punctatus* Fab. 21♂, 12♀, 2 sex not determined. *Onesia sepulchralis* L. 5♂. *Sarcophaga carnaria* L. 1♂, 1♀. *Pollenia rudis* Fab. 1♂. *Muscina stabulans* Fall. 1♂, 1♀. *Calliphora erythrocephala* Mg. 21♂, 12♀. *C. vomitoria* L. 2♂, 1♀. *Euphoria* sp. 1♀. *Lucilia* sp. 16♂, 7♀. *Polietes lardaria* Fab. 1♂. *Hytodesia errans* Mg. 1♀. *Anthomyia pluvialis* L. 1♂, 1♀. *Themira putris* L., *T. minor*, *Sepsis* sp., *Sciara* sp., a few examples.

We do not regard it likely to be of much value, at present, to publish the meteorological records kept in these preliminary experiments. The trials were not conducted on a sufficiently extensive scale to warrant any conclusions being drawn, with reference to the relations between weather conditions and insect behaviour. Furthermore, owing to the war we were unable to procure the necessary self-recording instruments. Without the aid of the latter, the data provided by the ordinary wet and dry bulb thermometer, for example, are of little comparative value, and could not be obtained during the night. The most noteworthy features of the experiments enumerated in the preceding pages may be summarised as follows.

1. The experiments were conducted during July and August 1918, and for the most part during wet and apparently unfavourable climatic conditions.

2. The insects attracted consisted almost exclusively of Diptera. With the exception of one or two examples of *Vespa vulgaris*, no Hymenoptera responded. Rhynchota, Coleoptera and Neuroptera (*sen. lat.*) were unrepresented. A small number of Noctuid Lepidoptera entered the traps, but for the purpose of conducting experiments with such relatively large insects, as many Lepidoptera, it would be necessary to slightly alter the construction of the traps used in order to allow of greater facilities for ingress.

3. Beer, cane molasses, and mixtures of these two substances are powerful chemotropic agents for various Diptera. Ethyl alcohol, in various concentrations, exhibited little or no chemotropic properties but with the addition of small amounts of butyric, valerianic or acetic acids it exercised a powerful stimulus. Aqueous solutions of the above acids were not attractive, the respective esters probably being the attractive agents in each case. The remaining substances utilised in these experiments were found to exhibit little or no positive chemotropic properties.

4. Out of considerably over 3000 Diptera attracted during the course of these observations, by far the greater number pertained to one or other of the five families Rhyphidae, Mycetophilidae, Sepsidae, Muscidae and Anthomyidae.

5. As a general rule members of both sexes of a species were attracted irrespective of the chemotropic agent employed. In the majority of instances males predominated over females, but in no case where the number of individuals of a species attracted exceeded 20 was the disproportion greater than 2·9 males to 1 female.

6. *Rhyphus punctatus*, *Hylemyia strigosa* and *Calliphora erythrocephala* were the dominant species attracted.

V. BIBLIOGRAPHY.

BARROWS, W. M. (1907). The Reactions of the Pomace Fly (*Drosophila ampelophila*) to odorous substances. *Journ. Exp. Zool.*, IV., pp. 515–37.

BUCK, J. E. (1915). Fly Baits. Circ. 32, *Alabama Agric. Expt. Sta.*

CHATTERJEE, N. C. (1915). Chemotropism; influence of Kusum oil on Insects. *Journ. Bombay Nat. Hist. Soc.*, pp. 198–99.

CRUMB, S. E. and LYON, S. C. (1917). The effects of certain chemicals upon oviposition in the House-fly. *Journ. Econ. Entom.*, X., p. 532–36.

DAVIDSON, J. (1918). Some practical Methods adopted for the Control of Flies in the Egyptian Campaign. *Bull. Entom. Res.*, VIII., pp. 297–309.

DEAN, G. A. (1915). Further Data on Poisoned Bran Mash flavoured with Fruit Juice as a means of controlling some Insects. *Journ. Econ. Entom.*, VIII., pp. 219–27.

DEWITZ, J. (1912). The bearing of Physiology on Economic Entomology. *Bull. Entom. Res.*, III., pp. 343–54.

FEYTAUD, J. and BOS, J. (1914). Observations sur l'emploi des pièges-appâts contre Eudémis. *Bull. Soc. Et. Vulg. Zool. Agric.*, Bordeaux, XIII., pp. 30–34 and 45–50.

—— (1914). La lutte contre la mouche de l'olivier en Italie. *Bull. bi-mens. Gov. Gén. Algerie*, XX., pp. 98–100.

FORBES, S. A. (1908). Experiments with repellents against the Corn Root Aphis. *Journ. Econ. Entom.*, I., pp. 81–83.

HOWLETT, F. M. (1912). The effects of oil of citronella on two species of *Dacus*. *Trans. Entom. Soc.*, pp. 412–18.

—— (1914). A Trap for Thrips. *Journ. Econ. Biol.*, IX., pp. 21–23.

—— (1915). Chemical reactions of Fruit Flies. *Bull. Entom. Res.*, VI., pp. 297–306.

IMMS, A. D. (1914). The Scope and Aims of Applied Biology. *Parasitology*, VII., pp. 69–87.

JARVIS, E. (1916). Combating the Cane Beetle. *Queensland Agric. Journ.*, V., pp. 169–70.

LODGE, O. C. (1916). Fly Investigations Reports. 4. *Proc. Zool. Soc.*, pp. 481–518.

—— (1918). An Examination of the Sense Reactions of Flies. *Bull. Entom. Res.*, IX., pp. 141–51.

LOEB, J. (1918). *Forced Movements, Tropisms and Animal Conduct.*

LUTCHNIK, V. (1914). Note on trapping insect pests. Reprint from *Friend of Nature*, published by the Section of Agric. and Exp. Organization of Kiev Soc. of Agric. and Agric. Industry. (Vide *Rev. App. Entom.*, 1914, A, p. 138.)

MOREAU, L. and VINET, E. (1913). Au sujet de l'emploi des pièges à vin pour capturer des papillons de la Cochylis. *C. R. Acad. Sci. Paris*, CLVII., pp. 1158–60.

MORRILL, A. W. (1914). Experiments with House-fly Baits and Poisons. *Journ. Econ. Entom.*, VII., pp. 268–74.

PARKER, R. R. (1918). Data concerning Flies that frequent privy vaults in Montana. *Entom. News*, XXIX., pp. 143–46.

RICHARDSON, C. H. (1916). A Chemotropic Response of the House Fly. *Science*, XLIII., pp. 631–16.

—— (1916). The Attraction of Diptera to Ammonia. *Ann. Ent. Soc. America*, IX., pp. 408–13.

RICHARDSON, C. H. (1917). The Response of the House-fly to certain Foods and their Fermentation products. *Journ. Econ. Entom.*, x., pp. 102–109.

SEVERIN, H. H. P. and H. C. (1913). An historical account of the use of Kerosene to trap the Mediterranean Fruit-fly. *Journ. Econ. Entom.*, VI., pp. 347–51.

—— (1914). The Behaviour of the Mediterranean Fruit-fly towards Kerosene. *Jl. Anim. Behav.*, IV., pp. 223–27.

—— (1914). Relative Attractiveness of vegetable, animal and petroleum oils for the Mediterranean Fruit-fly. *Journ. N. Y. Entom. Soc.*, XXII., pp. 240–48.

—— (1915). Kerosene Traps as a means of checking up the effectiveness of a Poisoned Bait Spray to control the American Fruit-fly. *Journ. Econ. Entom.*, VIII., pp. 329–38.

SEVERIN, H. H. P. (1918). Oils tested to trap Trypetidae and Ortalidae. *Journ. Bull. Calif. State Comm. Hortic., Sacramento*, VII.

SIMPSON, J. J. (1918). Bionomics of Tsetse and other Parasitological notes from the Gold Coast. *Bull. Entom. Res.*, VIII., p. 206.

TRAGARDH, I. (1913). On the chemotropism of Insects and its significance for Economic Entomology. *Bull. Entom. Res.*, IV., pp. 112–17.

TRYON, H. (1916). Bean Flies and other pests. *Queensland Agric. Jl.*, VI., pp. 34–35.

VERSCHAFFELT, E. (1910). The cause determining the selection of food in some herbivorous Insects. *Amsterdam Vers. Wis. Nat. Afd. K. Akad. Wet.*, XIX., pp. 594–600 (Dutch); *Proc. Sci. K. Akad. Wet.*, XIII., pp. 536–542 (English).

WASHBURN, F. L. (1912). The Minnesota Fly Trap. *Journ. Econ. Entom.*, V., pp. 400–402.

WEISS, H. B. (1912). Some economic methods a hundred years old. *Journ. Econ. Entom.*, V., p. 88.

ON FORMS OF THE HOP (*HUMULUS LUPULUS* L. AND *H. AMERICANUS* NUTT.) RESISTANT TO MILDEW (*SPHAEROTHECA HUMULI* (DC.) BURR.).

IV.

By E. S. SALMON,

Mycologist, S.E. Agricultural College, Wye, Kent.

In previous articles (1) (2) (3) it has been pointed out that resistance to the attacks of the mildew *Sphaerotheca Humuli* (DC.) Burr. is found in certain forms of *Humulus Lupulus* L., viz., (1) in a variety known to nurserymen as the "Golden Hop," and (2) in certain seedlings of the wild plant obtained from Italy. Experiments have now demonstrated the existence of a form of *H. americanus* Nutt. resistant to mildew. Our present knowledge with respect to these three groups of mildew-resistant hops is given below.

(1) The "Golden Hop."

Several distinct forms of *H. Lupulus* with yellow ("golden") leaves are on sale by nurserymen. These forms are quite distinct, and in several instances the stocks in nurseries have become mixed. The following information has been collected with respect to the characteristics, origin and name of these forms.

(1) Plants were obtained under the name of "Golden Hop" from Messrs Bunyard and from Messrs Bide and Son. In both cases the stock proved to be mixed, the plant sent being sometimes female and immune, and sometimes male and fully susceptible to mildew. Mr E. A. Bunyard has written to me: "I fancy our 'Golden Hop' came from Messrs Bide and Son, but no record was kept." Messrs Bide and Son wrote, in March, 1916: "We bought the plants in the first place from M. G. Bénard, Orleans, France. We do not claim to be the introducers of this plant, as we quite think it is to be had from other firms in this country." In Feb. 1918, Mr A. R. Bide wrote: "I cannot tell you definitely how many years we have listed this, but it is certainly 8 to 10. I first saw this growing in the nursery of Messrs Turbat et Cie, when I was at Orleans, and as I had never seen the Golden variety before, I bought some. Since

then we have worked a stock of our own." In answer to enquiries, M. Bénard wrote: "La variété *Humulus Lupulus aureus* m'a été fournie d'après ce que je crois me rappeler par M. Heerma Van Voss, pépiniériste à Oudenbosch (Hollande), ce qui explique que je n'en suis pas l'obtenteur"; and Messrs H. W. van der Bom and Co. (U. J. Heerma Van Voss) wrote: "our Mr Heerma has not introduced the Golden Hop (*H. Lupulus* var. *aureus*)." Messrs E. Turbat et Cie wrote: "We are not the originators of it."

It seems clear from the above information that one stock of the "Golden Hop" was imported from the Continent, and we may perhaps assume that it was at the time mixed, and consisted of an immune female plant—as to the origin of which I have not up to the present been able to obtain any information—and a susceptible male plant, which, as will now be shown, is probably to be identified as the *H. Lupulus aureus* described from Germany.

(2) Another stock of the "Golden Hop" in this country has been distributed from Messrs Dicksons, who very kindly supplied me with plants in 1917. With regard to the origin of this plant the firm wrote: "*H. Lupulus aureus* originated from a sport about 1893. It was discovered in a botanic garden in Germany and we bought half the stock which is very limited. We propagated and sent out 3 years afterwards (1896). It is propagated from shoot and root cuttings. The book containing the record has been destroyed. We issued a coloured plate of it, but the supply is now exhausted. This plate does not show the sex of the plant. We have so far as we know only the female form."

All the plants sent by Messrs Dicksons proved (in the greenhouse) to be susceptible to mildew, and those which flowered the next year in the hop garden (being the same individuals as those which were susceptible to mildew the previous year) all proved to be males. On acquainting Messrs Dicksons with the latter fact, the firm wrote: "Several of our Golden Hops are flowering this year but all are male plants."

Through help given by Prof. L. H. Bailey, it became possible to identify this male "Golden Hop" obtained from Germany. Prof. Bailey referred me to *Die Gartenwelt*, III, 1899, p. 476, from which I transcribe below the more important descriptive parts: "Neue Pflanzen. *Humulus Lupulus aureus* Von C. Bonstedt, Obergärtner des botanischen Gartens in Rostock....Als neuestes Goldkind, welches sich den Genannten ebenbürtig zur Seite stellt, führe ich heute den geschätzten Lesern eine Schlingpflanze und zwar einen Sport des allbekannten Hopfens (*H. Lupulus* L.) vor....*H. Lupulus aureus* ist bis jetzt nur in männlichen Pflanzen vorhanden....Aufgefunden wurde diese hübsche Form vor etwa zehn Jahren von Baumschulbesitzer Finck aus Doberan, der sie seitdem unablässig vermehrte und jetzt einen grossen Posten stattlicher Pflanzen besitzt, die die Firma J. C. Schmidt-Erfurt erworben hat....Die durch Sportbildung erzeugte goldgelbe Farbe ist somit durch ganz andere Faktoren bedingt als die der Herbstfärbung und hat gewiss auch mit der durch Nährstoffmangel hervorgerufenen Chlorose nichts zu schaffen, da auch üppiges Wachstum die Pflanzen nicht so leicht in die grüne Stammform zurückführt." The coloured plate accompanying the above description is entitled "*Humulus Lupulus aureus* (Goldenes Vliess)"; it shows no flowers. The plant is referred to again in *Die Gartenwelt*, x, p. 498 (1906), where the name "Goldhopfen" is proposed for it.

It seems clear from the information (given above) supplied by Messrs Dicksons that the plant distributed by them is the true *H. Lupulus aureus*. It is possible that the susceptible male golden hop which has become mixed up with the immune female golden hop in the stocks held by Messrs Bunyard and by Messrs Bide and Son is also the var. *aureus*, but I have not had the opportunity yet of comparing mature plants.

(3) A third form with "golden" leaves was brought to my notice by Mr Jesse Amos, Foreman Recorder at the Wye College Fruit Experiment Station at East Malling. This plant, which is growing in a garden at Malling, was obtained originally from Messrs J. Veitch and Sons, of Chelsea. I have not been able to obtain any information as to its origin. It is of the female sex; three cuttings taken from it in 1918–19 proved in the greenhouse during 1919 to be slightly susceptible to mildew. It is therefore different in constitution at any rate to the plant sent out by Messrs Bunyard and Messrs Bide and Son. I have not yet had the opportunity of studying mature plants of this susceptible female golden hop.

To summarise the facts: we have in cultivation in nurseries and gardens in this country three forms of the Golden Hop, viz. (1) an immune female Golden Hop; (2) a susceptible female Golden Hop; (3) a susceptible male Golden Hop, the true *H. Lupulus aureus*[1].

As previously reported in 1919 (2) the female "Golden Hop" from Messrs Bunyard and from Messrs Bide and Son has proved completely immune to mildew both in the greenhouse and when grown in the open in a manured hop-garden. During 1918 and 1919, 47 potted plants (from the two sources noted above) were grown in the greenhouse and repeatedly inoculated with *conidia* throughout the growing season; no trace of any infection resulted. The plants ("hills") in the hop-garden, of which nine were obtained from Messrs Bunyard and three from Messrs Bide, have all remained immune to mildew for the past three to seven years.

---

[1] In *The Hop Farmer* by E. J. Lance (1838), p. 157, the following appears: "*Varieties of Hop.*—There is another raised by Mr W. Paine at Farnham, having the appearance of the autumnal tint of the leaves, they are always 'in the yellow leaf'; indeed their appearance, compared with the red bine, or black knots, is very striking, the one being a dark blue, while the other is a light yellow green; this variety of hop branches out very much and yields a delicate coloured strobile." This "golden" variety does not appear to have been cultivated commercially.

This immune female Golden Hop lacks sufficient vigour of growth (due possibly to its possession of yellow, instead of green, leaves) to make it probable that it will ever be suitable as a commercial variety for hop-growers. With the object of trying to obtain a suitable green-leaved hop immune to mildew, "seed" was collected and sown in 1917 from a plant of the immune "Golden Hop" growing in the hop-garden at Wye College (obtained originally from Messrs Bunyard)—the male parent being unknown. In 1918 a counting of the seedlings in the three seed-boxes was made according to the colour of the first leaves, with the following results:

Box	Yellow leaves	Green leaves
1	49	56
2	63	59
3	58	63
	170	178

"Yellow" included several different shades of yellow; among "green" were various shades, including pale-green, but *not* yellowish-green.

The most vigorous of the above seedlings were planted out in the hop-garden in the winter of 1918–19, and during 1919 it could be observed that some seedlings were green-leaved (sometimes dark green) and some yellow (or "golden") leaved.

Other seedlings of the same origin were tested for susceptibility to mildew. These consisted of 68 seedlings raised from one plant of the Golden Hop (obtained originally from Messrs Bunyard) and 37 seedlings from another plant of the same origin. These seedlings were 2-year-old plants, non-flowering, in pots, and were kept during 1919 in the greenhouse and constantly subjected to inoculation by *conidia* throughout the season. Their behaviour towards the mildew was as follows:

	Immune	Susceptible
Seedlings of plant 1 ... (Ref. no. 1/17)	47	21
Seedlings of plant 2 ... (Ref. no. 3/17)	25	12
	72	33

Among the 21 "susceptible" seedlings of "1/17" there were (1) one plant "semi-immune," *i.e.* the plant showed no infection except that on one leaf there were five tiny pale spots on which a weak growth of conidiophores occurred; (2) one plant very slightly normally susceptible; (3) two plants very susceptible; while (4) the remaining plants were normally susceptible, inclining towards the slightly susceptible side.

Among the 12 "susceptible" seedlings of "3/17" two plants were slightly susceptible, with the production of normal, small patches of mildew; one plant was very susceptible; and the remaining plants were normally susceptible.

All the "immune" seedlings in both cases were entirely immune.

Among the above 105 seedlings there was a great difference of colour of the leaf; some seedlings were as "golden" leaved as the female parent; others had a normal green leaf; and intermediate shades occurred. No attempt was made to classify these seedlings on a leaf-colour basis, as owing to culture in the greenhouse there was a tendency for the green-leaved plants to acquire a pale- or yellowish-green tint due to the special conditions. It was clear, however, that there were some plants with green leaves and resistant to mildew under greenhouse conditions.

These 105 seedlings have been planted out in the hop-garden at Wye College, with the object of investigating them in the open in future seasons as regards (1) sex, (2) colour of leaves, (3) vigour of growth, (4) susceptibility to mildew, and (5) commercial value.

(2) SEEDLINGS RAISED AT WYE FROM SEED OF THE "WILD HOP" (*H. Lupulus*) OBTAINED FROM VITTORIO, ITALY.

In 1919 cuttings of certain seedlings of the above origin were grown in pots in the greenhouse and tested for resistance to mildew both by being surrounded throughout the season by mildew-infested hop-plants and also by direct inoculations with *conidia.* While, as in past seasons, numerous clone-plants of other seedlings of the same parentage and age and treated in the same way quickly became infested with mildew (which persisted on them throughout the season), the following seedlings proved to be immune, the entire plant remaining absolutely free from any trace of infection.

Four of the following seedlings (viz. Z 17, OY 18, II 24, II 30) had not been tested in this way before; the remaining 15 seedlings had shown the same resistance in previous seasons (see (3)).

Ref. no. of seedling	Number of clone-plants	Ref. no. of seedling	Number of clone-plants
V 91	1	OA 49	2
V 92	1	OB 34	10
V 93	1	OD 19	2
Z 2	2	OR 38	8
Z 14	2	OR 39	7
Z 17	1	OY 18	2
Z 22	2	HH 44	2
Z 25	3	II 24	2
Z 31	1	II 30	2
Z 42	2		53

All the above seedlings have been growing for several years in the Experimental Hop-garden at Wye College, and Table I shows the behaviour of each seedling, and also of four other seedlings of the same origin, towards the mildew (1) when the hop-plant is growing in the hop-garden, and (2) when a cutting is taken and grown in a pot in the greenhouse.

Table I.

		1917		1918		1919	
Ref. No.	Sex	In greenhouse	In hop-garden	In greenhouse	In hop-garden	In greenhouse	In hop-garden
316	?	0	—	0	—	—	S^1
V 91	♀	0	—	—	S^1	0	0
V 92	♂	0	—	—	S^1	0	0
V 93	♂	0	—	—	S^1	0	S^1
Z 2	♂	0	—	0	0	0	0
Z 14	♂	—	0	0	S^1	0	0
Z 17	♂	—	—	—	—	0	*
Z 22	♀	—	0	0	S^2	0	S^2
Z 25	♀	—	0	0	0	0	S^1
Z 31	♂	—	—	—	—	0	S^1
Z 42	♂	—	0	0	0	0	*
OR 38	♀	0	S^2	0	S^2 and S^3	0	S^1
OR 39	♂	0	S^1	0	0	0	0
OA 49	♀	—	0	0	0	0	0
OB 26	?	0	—	0	—	—	*
OB 34	♀	—	0	0	S^1	0	*
OD 19	♀	—	0	0	0	0	S^1
OE 14	?	0	—	0	—	—	*
OY 18	♂	—	—	—	—	0	S^1
DD 31	?	0	—	0	—	—	S^1
HH 44	♀	—	S^1	0	S^1	0	S^1
II 24	♂	—	—	—	0	0	0
II 30	♂	—	—	—	0	0	*

The figures 1 to 3 indicate the amount of mildew present; 1 = mere trace of mildew, 2 = fair amount of mildew, 3 = plant very mildewed. * signifies that no suitable material was available at the time when the observations were made (see below, p. 304).

Before we consider the significance of the *data* collected in Table I, we must note the behaviour towards the mildew of other seedlings of the same parentage and age. First, as regards the susceptibility shown in the hop-garden. In several cases we are able to compare the behaviour of seedlings growing by the side of, and close to, the "immune" seedlings of Table I; here the factors connected with soil, manuring, climatic conditions and exposure to infection by spores of the mildew are the same, so that any difference in susceptibility that is shown must be attributed to the different "constitutional" characters of the respective seedlings.

Table II.

Ref. No.	Sex	1917	1918	1919
Z 24	♀	S^3	S^3	S^3
Z 26	♀	S^3	S^3	S^2
Z 39	♀	S^3	S^3	S^3
Z 41	♀	S^3	S^2	S^3
Z 43	♀	S^2	S^2	S^1
OA 26	♀	S^3	S^3	S^3
OA 35	♀	S^3	S^3	S^3
OA 53	♂	0	S^2	—
OB 48	♀	S^3	S^3	—
OD 16	♀	S^3	S^3	S^3
OD 18	♀	S^3	S^3	S^3
OD 20	♀	S^2	S^1	S^1
II 11	♀	—	S^1	—
II 31	♂	—	S^3	—

Table II records the incidence of mildew during 1917, 1918 and 1919 on 14 seedlings growing in the hop-garden.

We see that the seedlings Z 24 and Z 26, which grew on either side of the "immune" Z 25 (and so closely that lateral shoots became intertwined) have each season[1] become excessively mildewed. Similarly with Z 41 and Z 43, on either side of, and as close to, the "immune" seedling Z 42; and with OD 18 and OD 20 on either side of OD 19.

We will now return to the consideration of Table I. Some further *data* are available with respect to some of the plants there tabulated.

The seedlings 316, OB 26, OE 14, DD 31 were subjected to the severest test (as regards constant inoculation with *conidia*) in the greenhouse during the seasons 1916, 1917 and 1918[2], and all remained persistently immune. On being planted out into the hop-garden in the winter of 1918–19, two of the seedlings (316, DD 31) showed in the autumn of 1919 a trace of mildew on their leaves; the other two seedlings were not able to be tested as to their susceptibility.

---

[1] In 1916 also both plants were S^3, while no mildew occurred on Z 25.

[2] See (1), p. 456; (2), p. 88; (3), p. 252.

The seedlings V 91, V 92, V 93 all completely resisted infection in the greenhouse during the seasons 1916 and 1917; the seedlings were planted out in the hop-garden in the winter of 1917–18, and the next season (Sept. 1918) each plant showed a trace of mildew on its leaves. Cuttings taken from each plant in the hop-garden in 1918–19 proved completely resistant in the greenhouse during the season of 1919, while one of the seedlings (V 93) in the hop-garden again showed a trace of mildew in Sept. 1919.

The seedling Z 22 was susceptible to the second degree in the hop-garden in both 1918 and 1919, while cuttings taken in 1918–19 proved to be immune in the greenhouse in 1919.

The seedling Z 25 is persistently immune in the greenhouse, and is usually immune in the hop-garden, although the two seedlings (Z 24, Z 26) on either side of it become severely mildewed each season. In June 1918 inoculations with *conidia* were made on the young leaves of Z 24, Z 25, Z 26, and infection resulted only on Z 24 and Z 26[1]. The circumstances attending the infection of Z 25 in the hop-garden in 1919 are discussed below (p. 306).

In 1918 one bine of OD 19—a strong lateral shoot arising about 5 ft. from the ground—twined round the bines of OD 18 and produced healthy hops intermingled with the excessively mildewed ones of OD 18. In 1919 a minute trace of mildew occurred in September on OD 19.

The seedlings OR 38 and OR 39 are immune in the greenhouse[2]; in the hop-garden susceptibility is shown, OR 38 being sometimes infected severely[3].

The seedling HH 44 has shown a trace of mould in the hop-garden each season in 1917, 1918 and 1919, yet cuttings taken both in 1917–18 and 1918–19 proved to be immune when grown in the greenhouse the next season.

The evidence appears conclusive that (1) seedlings which are immune when grown in the greenhouse may show susceptibility when grown in the open; that (2) the susceptibility shown by such seedlings in the open is as a rule slight; and that (3) cuttings taken from such seedlings after the latter have grown for several years in a manured hop-garden are immune to mildew when grown in the greenhouse.

---

[1] See (3), p. 254 for further details.

[2] See, however, (2), pp. 84, 86.

[3] In 1918 two plants of OR 38, in different parts of the hop-garden, were susceptible to the extent of S^2 and S^3 (see Table 1).

Although it seems clear from the above that the conditions of growth obtaining in the greenhouse are more favourable for the phenomenon of immunity than are those in the hop-garden, experiments have shown that it is only with seedlings of a certain "constitution" that the environment has this effect on the plant. If cuttings are taken from other susceptible seedlings (of the same parentage and age) in the hop-garden, and grown in the greenhouse, no approach is shown towards immunity. In the winter of 1918–19 cuttings were taken from the following seedlings, which had been affected with mildew during 1918 to the extent indicated: Z 24 (S^3), Z 26 (S^3), Z 39 (S^3), OA 26 (S^3), OA 35 (S^3), OA 53 (S^2), OB 48 (S^3), OD 16 (S^3), II 11 (S^1), II 31 (S^3). These cuttings were grown, and exposed to infection, in exactly the same way as the 53 cuttings of the 19 "immune" seedlings enumerated above at p. 298, and all quickly became infected and continued so throughout the season. Most exhibited what could be called normal susceptibility, but the seedlings Z 39, OA 26, and II 31 showed extreme susceptibility under greenhouse conditions.

In no case has any seedling of the wild hop from Italy which has proved immune in the greenhouse in any one season shown any susceptibility when tested in the greenhouse in other seasons[1]. Since this immunity in the greenhouse is correlated with some degree of, if not total, immunity when the plant is grown in the open, the index of reaction to mildew of hop plants in the greenhouse becomes a useful guide for the selection of mildew-resistant plants for the hop-garden.

In a previous article ((3), p. 256) cases of "semi-immunity" were recorded. Four seedlings were met with showing this phenomenon, viz. Z 15, OC 6, Z 23, and OA 33. During 1919 another "semi-immune" seedling, OD 17, was found. The behaviour of all these seedlings was studied both in the greenhouse and in the hop-garden.

---

[1] In 1918 a certain seedling (Ref. No. 8/16 I) raised from a seed collected from a plant of the "wild hop" of Canada (sent to me from Morden, Manitoba, in 1916 by Prof. W. T. Macoun) growing in the hop-garden at Wye College, remained persistently immune in the greenhouse throughout the season. This seedling was a 1-year-old plant of weak growth. In 1919 the seedling, still kept in the greenhouse, was slightly more vigorous, and produced two rather weak stems (1 ft. 9 in. and 1 ft. 6 in. in length), on most of the leaves of which small "powdery" patches of mildew appeared—the plant being clearly susceptible to a normal degree. The "wild hop" of Canada is probably *H. americanus* and the present seedling is therefore most likely of hybrid origin. A similar case to the above, where the seedling concerned was of hybrid (American) origin, has already been recorded ((3), p. 257).

The seedling Z 23, of which there were two cuttings in pots in the greenhouse, showed the nearest approach to immunity of the "semi-immune" group. The only visible sign of infection on the two plants after practically continuous inoculation by *conidia* for many weeks was the production of very small raised "blisters" or "humps," over the surface of which a very weak and evanescent growth of mycelium (never abundant enough to form a visible white layer) with a few conidiophores was produced. Thus no "powdery" patches were ever produced.

The seedling OC 6 (two plants) became more evidently affected by the attacks of the *conidia* than Z 23 was, and its leaves reacted in a very characteristic manner. The infection spots were larger, but again the mildew never produced enough mycelium to be white and conspicuous, and conidiophores were never produced abundantly enough to cause a "powdery" patch. On the death of the mildew, which soon took place, the leaves showed a distinct injury (confined to the places where the mildew had existed) in the form of conspicuous yellowish-brown blotches (closely resembling those found on the leaves of certain plants attacked by *Eriophyes* (Leaf "Blister-mites")).

With Z 15 (two plants) inoculation produced on the leaves a distinctly white and more or less "powdery" conidial patch, which, however, soon died away, exposing to view a conspicuous brown spot, composed of a group of affected epidermal cells.

The seedlings OA 33 (two plants) and OD 17 (two plants) showed also very similar infection-phenomena, but with less injury caused to the epidermal cells. These two seedlings may perhaps best be put in the susceptible class, although they show a tendency towards semi-immunity.

With the seedling BB 5 inoculation was followed by the production of small patches of mildew, white and powdery, but these patches remained small and isolated, not increasing in size and becoming confluent as on the leaves of plants showing full susceptibility.

The behaviour of the above seedlings in the hop-garden during past seasons is shown in the table on p. 303.

My field-notes for the seedling OD 17 in the hop-garden were as follows: "1917. Showed considerable resistance to mould, producing a good crop of healthy hops, while OD 16 and OD 18 (two seedlings of the same parentage and age), growing on either side and so close that lateral shoots intermixed, were so infected with mould that they produced no healthy hops. 1918. Mere trace of mould on the hops; OD 17 is obviously of quite different 'constitution' from OD 16 and OD 18, whose laterals bearing very mouldy hops grew in among the lateral shoots of OD 17 which bore a crop of hops practically immune from mould."

Table III.

		1917		1918		1919	
Ref. No.	Sex	In greenhouse	In hop-garden	In greenhouse	In hop-garden	In greenhouse	In hop-garden
Z 15	♂	—	S^2	"semi-immune"	S^2	"semi-immune"	S^2
Z 23	♂	—	S^2	,,	0	,,	S^1
OC 6	♂	—	0	,,	0	,,	S^1
OA 33	♂	—	0	approaching "semi-immune"	0	approaching "semi-immune"	S^2
OD 17	♀	—	S^1	—	S^1	,,	S^1
BB 5	♀	—	—	—	S^1	,,	0

There appears to be evidence, then, that the physiological or "constitutional" characters which underlie the phenomenon of "semi-immunity" remain constant for the particular seedling, just as do those which account for complete immunity or susceptibility.

The phenomenon of "semi-immunity" has been met with in other seedlings of widely different parentage.

In the case of two seedlings (now planted out in the hop-garden under Ref. nos. 222 *a* and 236 *a*) studied in the greenhouse during 1919, infection scarcely proceeded further than the formation of small "humps" or "blisters," over which a scanty growth of hyphae occurred (never white in the mass), with a weak growth of conidiophores. The mildew soon died away, and exposed to view a patch of the underlying epidermal cells which had turned brown. Exactly the same phenomenon was observed with one of the seedlings in 1918. Both these seedlings were raised from seed collected by me in Sept. 1916 from a hop-plant growing wild on the sea-cliff at Salcombe Regis, near Sidmouth, Devonshire.

Another form of "semi-immunity" was met with (under greenhouse conditions) in a seedling (now Ref. no. 256 *a* in the hop-garden) raised from seed collected in 1916 from a plant of the variety *neo-mexicanus* planted in the hop-garden at Wye College—the male parent being unknown. Here inoculation is followed by the production of a weak growth of mycelium, scarcely white or "powdery," which soon dies away, leaving pale-green or yellowish, semi-translucent patches of leaf-tissue at the places where the mildew had previously existed. I have seen somewhat the same phenomenon, although not so marked, in the case of the var. *neo-mexicanus* itself, when grown in the greenhouse.

In my last communication ((3), p. 253) mention was made of a group of seedlings, five in number, which for several seasons had remained immune both in the greenhouse and hop-garden. During 1919, while clone-plants of all these five seedlings remained persistently immune in the greenhouse, two of the seedlings, viz. OD 19 and Z 25 showed in the open a very slight susceptibility. Of the remaining three seedlings, two (Z 2, OA 49) still proved immune in the hop-garden, while in the case of the other, Z 42, no young growth was available in the autumn to test its susceptibility.

The circumstances under which those seedlings which are immune in the greenhouse show in the open, in some seasons, an approach towards susceptibility are worthy of study. The susceptibility shown has been noticed in past years only late in the season, in September or early October, when the plant is commonly exposed to adverse conditions of growth such as low temperatures at night, or cold rains or mists. In order to try to obtain some evidence as to which among the various cultural conditions are the determining ones with regard to the breaking down of immunity to mildew when the plant is grown in the open, cuttings of certain seedlings (all potted up in the same kind of soil) were treated in three different ways. Those in Group I were placed in the greenhouse in the autumn of 1918 and kept there throughout the season of 1919; those in Group II were kept in the open through the winter and spring until June 2 (by which time the plants had produced shoots 2 to 3 ft. long) when they were placed in the greenhouse and exposed to infection; in Group III the plants stood in the open with those of Group II until June 2, when they were placed in the hop-garden (with the pots standing in saucers so that no food could be absorbed from the soil). The seedlings which were used may be divided into three classes: *a*, those which remain persistently immune when grown in the greenhouse; *b*, those which are "semi-immune" in the greenhouse; *c*, those which are decidedly susceptible (all S^2 or S^3) when grown in the hop-garden. The number of clone-plants used is given in brackets.

Group 1.—Greenhouse throughout.

Class a. OR 38 (8); OR 39 (7); Z 25 (3); V 91 (1): V 92 (1); V 93 (1): Z 42 (2); Z 2 (2); Z 14 (2); Z 17 (1); Z 31 (1); OD 19 (2); Z 22 (2); HH 44 (2); OA 49 (2); OB 34 (10). "Golden Hop" (from Messrs Bide (6), from Messrs Bunyard (2)).

Class b. Z 15 (2); OC 6 (2); OA 33 (2); Z 23 (2); OD 17 (2).

Class c. OA 36 (1); Z 39 (1); OA 35 (1); OA 26 (1); OA 34 (1); H 31 (1); OB 48 (1); OD 16 (1); Z 24 (1); Z 26 (1).

Group II.—Outside—later moved into greenhouse.

Class a. OR 38 (6); OR 39 (7); V 91 (1); V 93 (1); Z 42 (1); Z 2 (1); Z 14 (1); OD 19 (2); HH 44 (1); OB 34 (10). "Golden Hop" (from Messrs Bide (6), from Messrs Bunyard (2)).

Class b. OC 6 (1).

Group III.—Outside—later moved into hop-garden.

Class a. OR 38 (11); OR 39 (8); Z 25 (3); V 91 (1); V 92 (1); V 93 (1); Z 42 (2); Z 2 (2); Z 14 (2); OD 19 (3); Z 22 (2); HH 44 (2); OA 49 (2); OB 34 (10); Z 17 (1); Z 31 (1). "Golden Hop" (from Messrs Bide (8), from Messrs Bunyard (2)).

Class b. Z 15 (2); OC 6 (2); OA 33 (2); Z 23 (2); OD 17 (1).

Class c. OA 36 (1); Z 39 (1); OA 35 (1); OA 26 (1); II 31 (1); OB 48 (1); OD 16 (1); Z 24 (1); Z 26 (1).

The plants in Group I behaved as follows:

Class a. All the plants remained persistently immune.

Class b. All the plants proved "semi-immune" (see p. 302).

Class c. All the plants quickly became fully infected, OA 26, Z 39, and II 31 being noted as becoming virulently infected.

The plants in Groups II and III were examined on June 13th, up to which date they had stood together in the open outside the greenhouse; all the plants in Class *a* of both Groups were healthy; of those in Class *b*, one plant of OA 33 showed in a typical form the phenomenon of "semi-immunity," and on one plant of OD 17 there was a *very* minute "powdery" patch on two of the leaves; the remaining plants were healthy. In Class *c*, more or less numerous, small patches of mildew (from natural infection) occurred on all the plants, with the exception of OA 36.

The plants of Groups II and III were then placed, respectively, in the greenhouse or in the hop-garden.

In the greenhouse the plants of Group II, Class *a* remained as persistently immune as those of Group I, Class *a*. The experiment shows, then, that the immunity of such seedlings as these is not dependent on the plants *having been raised* under greenhouse conditions, but is maintained when plants with shoots 2–3 ft. high produced in the open are taken into the greenhouse. Similarly, the seedling OC 6 in Group II, Class *b* showed the phenomenon of "semi-immunity" when taken into the greenhouse and inoculated.

With regard to the plants of Group III, no mildew was noticed on the plants in Class *a* up to the end of September. The frosts which occurred early in October shrivelled up the leaves of many of the plants, but on October 23, when an examination was made of all the plants still possessing young green leaves, one plant of OR 38 was found to be infected very slightly, there being a tiny "powdery" patch on the undersurface of two of its leaves. Since the eight clone-plants of OR 38 kept entirely in the greenhouse and the six clone-plants taken into the greenhouse on June 13 (of the same age and potted up in the same soil) all remained persistently immune in spite of repeated inoculations, while one of the 11 clone-plants exposed in the hop-garden to natural infection showed this susceptibility late in the autumn (after frosts), it appears safe to draw the inference that the immunity of such seedlings as OR 38 is broken down, or partly broken down, by certain climatic conditions—possibly low temperature.

Certain facts, observed in the hop-garden during 1919, with regard to the behaviour of Z 25 tend to support the above view. This seedling, Z 25, was originally planted out in the hop-garden in 1914. Each season from 1916 to 1918 it remained immune to mildew, although similar seedlings (as regards origin and age) on either side of it became severely mildewed (see above, p. 299). In 1918 young leaves of Z 25 (in the hop-garden) were artificially inoculated in June, and proved completely resistant. In 1919, for the first time in the history of Z 25, a few small mildew-patches were observed on the plant in the hop-garden; this occurred on Aug. 7. The mildew-spots were on the young leaves of lateral shoots at about five feet from the ground. The mildew-affected leaves were allowed to remain on the plant, but by September all the mildew-patches had died away on these leaves, and no mildew could be found elsewhere on this plant. In early October when the plant was examined carefully, together with some hundreds of seedlings of the same parentage—most of which were severely affected with mildew—not a trace of mildew could be found on the leaves or hops of Z 25—notwithstanding the fact that laterals of the adjacent plant Z 26 had twined round the bines of Z 25 and produced hops covered with mildew among the immune hops of Z 25. The slight susceptibility shown by Z 25 in August 1919 was temporary and was caused, apparently, by some special conditions of growth. It is most probable that these conditions were climatic. Just previously to the susceptibility being shown, there was a pronounced spell of cold, and wet or dull weather, abnormal for the time of year. As soon as normal, warm and sunny weather prevailed, the patches of mildew on Z 25 died away, without any further infections having taken place, although on other seedlings of different "constitutions" the mildew prevailed and increased up to the middle of autumn[1].

---

[1] The Monthly Weather Reports of the Meteorological Office for the months of June to September, 1919, were as follows: "*June.* Sunny and Warm at first, then Cool and

Seedlings which have been raised from Z 25 have shown interesting deviations from normal susceptibility to mildew. The "seed" was collected in 1917 from the plant of Z 25 growing in the hop-garden at Wye College—the male parent being unknown. In 1919, 33 of these seedlings (Ref. no. 4/17), 2-year-old and non-flowering, were grown in pots in the greenhouse and constantly exposed throughout the season to inoculation by *conidia*. The behaviour of the seedlings was as follows:

Immune Seedlings	Susceptible Seedlings
24	9

The immune seedlings were all entirely immune.

The susceptible class comprised seedlings showing very different degrees of susceptibility. One seedling was very susceptible and another was normally susceptible—in both cases large "powdery" patches being produced by the mildew soon after inoculation. The third seedling was very slightly normally susceptible—that is to say, the few infection-spots produced consisted of normal "powdery" patches. The fourth seedling might have been termed "semi-immune," except that occasionally effused "powdery" patches were formed. The fifth, sixth, and seventh seedlings were all similar, and were apparently "semi-immune," in the sense in which this term is used above at p. 302. The last two seedlings presented new types of susceptibility not previously found in seedlings of the wild hop. In one seedling the slight susceptibility shown was manifested by the production of scattered conidiophores diffused over the

---

Rainy. Temperature: In England South-East the departure from normal was as small as +0·1*a*. The monthly aggregates of rainfall were below the normal. *July*. Cold generally; Dull in England. The mean monthly temperature was below the normal in all districts. The rainfall was below the normal, although the shortage in England South-East was only 1 mm. *August*. Many Hot days; Rainfall moderate; Sunshine abundant. Some warm days during the first part of the month were nearly balanced by some cold ones during the latter part, so that the mean for the month in most districts did not differ very largely from the normal."

The weekly deviation from Normal of the Mean of the Temperature of the Air (in degrees Fahrenheit) at the recording stations in S.E. England nearest Wye was as follows:

Recording Station	June 8 to 14	June 15 to 21	June 22 to 28	June 29 to July 5	July 6 to 12	July 13 to 19	July 20 to 26	July 27 to Aug. 2	Aug. 3 to 9	Aug. 10 to 16	Aug. 17 to 23
Tun. Wells	+3·5	+1·0	−5·5	−7·7	−3·7	−3·1	−4·3	−2·4	+0·7	+6·4	+3·4
Margate	+4·7	+3·0	−4·4	−5·4	−5·3	−1·4	−3·6	−2·9	+1·1	+6·3	+4·2
Dungeness	+1·7	−1·1	−5·1	−5·0	−3·5	−5·0	−4·1	−5·1	−1·2	+1·5	+1·3

There seems evidence then, for considering the temporary susceptibility shown by Z 25 at the beginning of August as an effect on the "constitution" of the plant caused by the abnormally low temperatures obtaining at the end of June and throughout July.

surface of the leaf; these conidiophores were not sufficiently aggregated anywhere to form a white "powdery" patch—indeed, in most places, they could only be seen when the leaf-surface was examined carefully in a good light. In the ninth seedling infection resulted in the production of pale blotches (scattered over the leaf) on which a weak growth of mycelium and conidiophores took place.

All the above "4/17" seedlings have been planted out in the hop-garden, so that their behaviour in the open with regard to susceptibility to mildew can be studied.

3. A FORM OF *H. AMERICANUS* (♂).

In 1914 Dr W. W. Stockberger, of the U.S. Department of Agriculture, sent me cuttings of an American hop, labelled 7 A, 7 C, 7 H. One plant, labelled 7 A, proved during 1918 in the greenhouse to be persistently immune to mildew. During 1919 the same plant of 7 A, together with six other cuttings taken during the winter of 1918–19 from clone-plants of 7 A growing in the hop-garden at Wye College, were exposed constantly in the greenhouse to infection by *conidia* throughout the season. All the seven plants remained entirely free from mildew. Cuttings of 7 C (two plants) and 7 H (one plant) taken at the same time from plants in the hop-garden, and treated in the same way in the greenhouse, proved susceptible—7 H being susceptible to a normal degree, and 7 C being very susceptible.

The above plants were sent to me by Dr Stockberger labelled "Golden Cluster"—which is a commercial variety of hop cultivated in the United States. While, however, the single plants of 7 C and 7 H which have flowered have proved to be pistillate and doubtless belong to the variety "Golden Cluster," all the (three) plants of 7 A which have flowered are staminate. This male plant certainly belongs to *H. americanus* and not to *H. Lupulus*, as it agrees in every way with the former species, which, as has been pointed out(4), is easily distinguished by the male inflorescence. Dr Stockberger has sent me the following information: "I am surprised to learn that the plants I sent you of my Number 7 A (Golden Cluster) all proved to be staminate. The original plant Number 7, from which cuttings 7 A, 7 B, 7 C and 7 H were taken, was obtained by me from a hop-field at Cosumne, Cal., Feb. 25, 1907. The original plant Number 7 was set in my hop-garden here at Washington, D.C., where it regularly bore good hops up until the time the clones were obtained and sent to you. At the same time the cuttings were sent to you, duplicates were re-planted in my garden here. My garden records show that these clones did not do very well, and that at present only three plants of Number 7 A remain. These, however, are all pistillate plants and have regularly borne a few clusters of hops. You can see therefore that I am quite at a loss to account for your staminate plants under Number 7 A."

The only references that I have been able to find on the subject of the resistance to mildew shown by different varieties of hops in the United States are the statements made by Prof. F. M. Blodgett. In 1913 this author wrote (5): "Thus it happens that the disease may not appear on the Cluster hop—the leaves of which appear to be more resistant than do those of the Canada, or red-vine, variety—until flowering time, when the mildew often spreads rapidly through the yards of Cluster hops, attacking the young flowers and later the hops." In 1915, Prof. Blodgett wrote (6): "Different varieties and even different leaves on the same plant vary in susceptibility. Named in order of susceptibility beginning with the most susceptible, the New York varieties would be arranged as follows: Canada red vine, English cluster, Humphrey and native red vine. No serious injury has been noticed, so far, on the native red vine variety though planted near badly infested yards and, in some instances, scattered through yards of a susceptible variety. It is said to be a light yielder, however." In a letter, dated Feb. 4, 1918, Prof. Blodgett wrote to me as follows: "I have found in the vicinity of Milford, Cooperstown, and East Springfield, in New York State, one variety of hops, the so-called 'Native Red Vines,' which appear almost entirely immune to the mildew. I have frequently seen yards in which this variety was mixed with very susceptible varieties, where the vines intertwine in many places, and still the Native Red Vine hops remained immune. Unfortunately, however, this hop is not a very desirable variety being a rather light yielder and has not appealed on that account to the growers. In 1914 a fellow in this department attempted making crosses between this and the more desirable commercial varieties in order to secure a good variety that was immune to the malady, but unfortunately this work was discontinued and was never completed."

SUMMARY.

1. Several forms of *H. Lupulus* with yellowish-green ("golden") leaves exist. One form (♀) has proved persistently immune to mildew both in the greenhouse and in the open. A second form (♀) has proved slightly susceptible when grown in the greenhouse. A third form (♂)

is susceptible in the greenhouse and in the open. This ♂ form appears to be the one found originally in Germany and described under the name of *H. Lupulus aureus*. No account of the origin of any ♀ "Golden hop" has been found in horticultural literature.

2. Certain seedlings raised from the immune ♀ "Golden hop" (the ♂ parent being unknown) possess green leaves and are immune to mildew when grown in the greenhouse.

3. Different seedlings of the wild hop (*H. Lupulus*) have distinctive physiological or "constitutional" characters, which are constant under the same environment. These characters confer immunity or susceptibility, or intermediate grades of susceptibility, on the respective seedlings. The immunity is retained by the plant after four years' residence in the manured soil of the hop-garden.

4. Certain seedlings of the wild hop which show persistent immunity when grown in the greenhouse show some degree of susceptibility when grown in the open. The susceptibility shown is usually very slight. There is some evidence that this breaking down of immunity is due to the effect of certain climatic conditions.

5. In the great majority of cases, the greenhouse conditions do not have the effect of making seedlings of the wild hop immune to mildew. In the case of some seedlings extreme susceptibility is shown under greenhouse conditions.

6. The phenomenon of semi-immunity is shown by certain seedlings of various origins.

7. A form (♂) of *H. americanus* Nutt., obtained from the United States, has proved immune to mildew under greenhouse conditions. Under the same conditions several American cultivated varieties proved susceptible.

BIBLIOGRAPHY.

(1) Salmon, E. S. On Forms of the Hop (*Humulus Lupulus* L.) resistant to Mildew (*Sphaerotheca Humuli* (DC.) Burr.). *Journ. Agric. Science*, viii, 455–460 (1917).

(2) —— *Idem*, ii. *Journ. Genetics*, viii, No. 2, 83–91 (1919).

(3) —— *Idem*, iii. *Annals of Applied Biology*, v, 252–260 (1919).

(4) —— and Wormald, H. *Humulus americanus* Nuttall. *Journal of Botany*, 1915, p. 132.

(5) Blodgett, F. M. Hop Mildew. *Cornell Univ. Agric. Exper. Station Bull.*, 328, p. 291 (1913).

(6) —— Further Studies on the Spread and Control of Hop Mildew. *N. York Agric. Exper. Station Bull.*, 395, p. 42 (1915).

ON THE SEXUAL FORMS OF *APHIS SALICETI*, KALTENBACH.

By MAUD D. HAVILAND,

Fellow of Newnham College, Cambridge.

In June 1919, while collecting numbers of *Aphis saliceti*, Kalt., from the sallow tree (*Salix caprea*) for the study of their hymenopterous parasites, it was found that the material chiefly consisted of sexual males and females, not of parthenogenetic individuals as might have been expected at that season. It is known that this aphis differs from most Aphidinae in the appearance of the sexuales at mid-summer instead of in the autumn, and their occurrence at this season has been observed both on the Continent and in America[1]. But hitherto they do not seem to have been recorded in this country, and as, so far as I know, there is no detailed description of these forms, one is appended.

There is some discrepancy in the earlier accounts of this species. Von Baehr (*Archiv. Zellforsh.*, 1919), who found the sexuales in Germany in May, says that Kaltenbach and de Geer also observed their appearance in summer; but reference to Kaltenbach (*Monographie der Pflanzenlausen, Aphiden*, p. 131) shows that this observer did not find them himself, though he records that de Geer found summer sexuales of *Aphis salicis*, which from the description is certainly a synonym for *Melanoxanthus salicis*, Buckt. Von Baehr supposes that this is a confusion (*Verwechselung*) between the two species, but from de Geer's description (*Memoires*, III., 11, 76) it is possible that the latter was in fact speaking of *Melanoxanthus*. He remarks on the row of white spots on the body, "puceron du saule aux taches cotonneuses," and describes the type as "obscure viridis, tuberculis lanuginosis albis, corniculis longioribus." The long cornicles apply better to *Aphis saliceti* than to *Melanoxanthus salicis*, but the pilose white patches cannot possibly refer to the former species; and Kaltenbach, who was acquainted with both forms, accepts de Geer's *salicis* as synonymous with his own. De Geer describes the male as dark yellow. Thus the possibility suggests itself that *Melanoxanthus*, which, so far as is known, is likewise a monophytophagous species of the willow, may sometimes produce its sexuales in June; and if this should prove to be the case, it would be an interesting point that two species of different genera on the same host plant should both produce their sexuales at this unusual season. The sexuales of *Melanoxanthus* have not been described, though Mordwilko (*Biol. Centralbl.*, 1907, p. 533) says he found them in August and September. The life-cycle of this species requires further investigation.

---

[1] 1906. Stevens, N. M. *Carnegie Institute, Wash., pub.* 51.
1918. Gillette, C. P. and Bragg, L. C. *Can. Ent.*, Vol. L., no. 3.

Parallel instances of the appearance of the sexuales in the summer are rare. Buckton (*Monograph of British Aphides*, II., p. 149) records that he found the sexuales of *Macrosiphum muralis* on *Lactuca* in the first week of July, but the females had then no eggs; and Koch says that the males of *Myzus persicae* occur in May, but, as Buckton and other observers have found the sexuales of this species in the autumn, it is possible that Koch's identification was incorrect. These seem to be the only similar cases on record; but it is possible that, with further study of the life-cycles of different aphides, the appearance of the sexuales in summer will prove to be more frequent than is now supposed, and that the disappearance of some forms, which is at present attributed to the migration of a biphytophagous species to the second host plant, will prove to be part of the normal cycle of a monophytophagous species after the production of fertilised ova. If so, as is actually the case with *Aphis saliceti*, the race can have at most but two or three months of active life: the rest of the year it exists in a dormant condition as an egg.

This species is dimorphic in respect of the parthenogenetic generations. The colour ranges from dark green to orange brown with intermediate varieties. This dimorphism extends to the sexuales, but here I found that the predominant colour for males was brown, and for females green.

The male.

Apterous. Short, oval. Length = ·92 mm. Breadth of abdomen = ·50 mm. Head, dusky. Eyes, reddish brown. Total length of antenna = 1·00 mm., colour, dark brown, with numerous small supplementary sensoria on segments III, IV, V. Thorax and abdomen, orange brown (rarely green), with a few darker markings on the dorsum. Genital plates dusky. Cauda, pale brown (or green). Cornicles, pale brown (or green), with dark imbricated scales, length = ·28 mm. Legs, pale brown, very long and stout, with stiff hairs on femora and tibiae. Tibial joints and tarsi dusky.

The oviparous female.

Apterous. Long, elliptical. Posterior segments elongated. Length = 1·8 mm. Breadth of abdomen = ·83 mm. Head, dusky. Eyes, brown, and somewhat deeply set. Total length of antenna = ·90 mm., colour, dark brown, without supplementary sensoria. Thorax and abdomen, dark green (rarely brown), sometimes with darker markings on the dorsum. A pair of lateral tubercles present on segments 1–4, 6. Cauda, green (or brown). Cornicles, green (or brown), with imbricated scales, length = ·27 mm. Legs, short and hairy, pale brown, tarsi black. Hind tibiae somewhat swollen, and bearing a few minute sensoria. Each female lays from three to five elliptical eggs on the bark of the shoots, or more rarely, on the leaves. The egg, which is at first yellow and translucent, soon becomes black and polished on exposure to the air.

PROCEEDINGS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS.

The Annual General Meeting was held in the Botanical Department. Imperial College of Science, on Wednesday, 10th December, 1919.

There were present 32 members and 15 visitors.

In the unavoidable absence of the President and the Vice-Presidents, the chair was taken by Mr E. E. Green.

The Minutes of the preceding meeting were read and confirmed.

Report of the Council for 1919.

During the year 1919 two general meetings have been held in the Botanical Department, Imperial College of Science, one in March and the other at the beginning of July, the latter occupying two days. They were both fairly well attended and numerous exhibits were made and important papers read.

At the latter meeting the resolutions of your Council on certain proposals made by Prof. Lefroy and Mr Brierley that had been circulated to all members in this country were passed.

Arising out of these a Botanical Secretary has been appointed in the person of Mr W. B. Brierley and steps are being taken to form a permanent Committee, of which Prof. Lefroy has consented to become a member, the duties of which *inter alia* will be to look after the interests of duly qualified Economic Biologists.

The membership of the Association shows a steady and satisfactory increase. Only one member has resigned and 13 have been elected during the year. In addition to this over 60 further members for 1920 have been nominated by the Council and their names will be placed before you at this meeting. If these are elected, they will bring our total membership from all sources up to over 200, as compared with 126 this time last year.

The publication of the *Annals of Applied Biology* in common with nearly all other scientific journals of this character has been considerably delayed, but Parts II and III of Volume VI may be expected to appear almost immediately and material for the remaining part is in hand.

The enormous increase in the cost of production of the *Annals* has been a source of considerable anxiety. With a view to improving the position the following recommendations by the Publication Committee have been approved by your Council.

(1) The reduction of the discount to American agents from 33⅓ per cent. to 15 per cent.

(2) The increase of the price to the public from 7*s.* 6*d.* per Part and 25*s.* per annum to 10*s.* and 33*s.* 6*d.* respectively.

(3) That an attempt should be made to obtain financial assistance from outside sources.

The Report was adopted on the motion of Dr Paine, seconded by Mr Bewley.

A statement as to the financial position of the Association was read by the Treasurer.

The names of 69 new members who had been nominated by the Council for election to the Association were read by the Secretary.

No further names having been received, the officers and Council, a list of whom had been circulated to all members in this country, were declared elected.

EXHIBITS.

Mr A. D. Cotton exhibited photographs received from the Office of Forest Pathology, Bureau of Plant Industry, Washington (D.C.), showing *Cronartium cerebrum* on *Quercus rubra* and *Pinus virginiana*, *Coleosporeum carneum* on *Vernonia* and *Pinus palustris*, and also a fine series of the chestnut bark canker caused by *Endothia parasitica.* Some discussion took place as to the history of *Endothia* in America and the likelihood of its being introduced to other countries.

Mr W. F. Bewley exhibited specimens of the following fungi:

On Tomato fruits.

(1) Showing a type of hard brown rot caused by *Penicillium* sp.

(2) Showing a soft white rot caused by a bacillus.

(3) Rot produced by *Botrytis* sp.

(4) Late season fruit attacked by *Macrosporium* sp.

(5) Showing "Stripe" lesions caused by *Bacillus lathyri.*

On Tomato stems.

(6) Attacked by *Botrytis* sp. at a jagged leaf base.

(7) "Stripe" lesions caused by *Bacillus lathyri.*

(8) Base of plant killed by "Sleepy Disease," showing the *Diplocladium* stage.

Mr E. E. Green exhibited specimens of *Stephanitis rhododendri*, together with rhododendron leaves injured by the insects. He remarked that this pest was a comparatively recent introduction, but was firmly established in Surrey and some other of the southern counties. In his own garden, Mr Green had observed that injury was confined to plants of the poorer varieties, especially such as had small, hard foliage. The insects lived on the under-surface of the foliage, but their presence was indicated by a reddish brown discoloration upon the upper surface of the leaves.

PAPERS.

The following papers were read and discussed:

Mr W. F. Bewley. "Sleepy Disease of Tomato."

Mr W. E. Hiley. "A new Method of measuring the Light Intensity in Woods."

Mr F. R. Petherbridge. "The Life-history of the Strawberry Tortrix (*Acalla comariana*)."

On Thursday, Dec. 11th, 1919 a Symposium on "The Integration of Mycological Research with Practice in Agriculture, Horticulture and Forestry" was held. The chair was taken by Professor Keeble, F.R.S. There were present 44 members and 16 visitors.

I. THE ADMINISTRATIVE PROBLEM.

By Sir A. D. HALL, K.C.B., F.R.S.,

Chief Scientific Adviser to the Ministry of Agriculture and Director-General of the Intelligence Department.

The problem I have to put before you this morning is that wider one of the relation between research and government departments. There has been much talk recently of the value and need of research and of the necessity for the country to take more interest in research than it has done in the past. In the past there has been little research it is true, but that little has been good and at present in our effort for reconstruction we must beware of the danger of introducing a state king stork instead of a king log.

We may assume that research will not pay its way and therefore must be supported by state funds, which of necessity means a certain amount of state supervision of the expenditure of the money. The power of the purse unfortunately confers a certain amount of control and can be made to carry with it complete control.

The Government Department, in this case the Ministry of Agriculture, has a strong technical side, which however ought to be still stronger. This is chiefly concerned with such investigation into disease in animals and plants as is required for the formulating and carrying out of the necessary regulation for such disease. For example the outbreak of disease may be isolated and so checked by the method of quarantine. This is an old idea and in the past has been carried out by the slaughter of the animals or plants, which method can be carried out without scientific advice. It is a simple process and one dear to administrators. But investigators have suggested more economical and efficient methods than the wholesale slaughter of diseased and contacts. With animal diseases there is compulsory treatment; with plant diseases compulsory spraying. These regulations are imposed on the community and there must be inspection to ensure that they have been carried out in an efficient way. We may instance compulsory spraying as a precautionary measure imposed either by legislation or by agreement as in continental vineyards. Such a measure must be imposed by a central department and it is obviously essential that this central department be adequately advised; it must therefore be in a position to carry out investigations to determine the value of the methods recommended. This is the immediate business of the department and the department must have research workers to whom it can look for advice.

Beyond this administrative end however is the fundamental work, the pursuit of knowledge for its own sake. This is "free" research as distinguished from "administrative" research. Men carrying out administrative research often have to range so widely afield that they do not see the need for further free research, and think that all research might as well be carried out under the government department. But this is a fundamental mistake, for a government department is unfitted by its very nature to conduct fundamental research.

In the first place governmental expenditure is subject to the closest scrutiny and criticism by non-expert bodies. Research expenditure is always liable to be overhauled by bodies such as the Treasury, the Public Accounts Committee, and the Committee on National Expenditure, *i.e.* expenditure has to be justified before non-expert bodies charged with the sole task of cutting down expenses. As an example one may adduce the reports of the United States Committee on Appropriations where you may read of the sorry spectacle of the scientist trying to justify his scientific research before them. Economic research has to justify itself in the long run by results, but it should be judged by its peers.

Such a situation reacts inevitably upon the scientific man himself. In self-protection he is driven to produce hypothetical balance sheets and to advertise himself. He is tempted to take a short point of view and not only to do work which will give immediate results but to produce these results very early. Awful examples can be quoted. Agriculture progresses in yearly cycles. The first year's investigation results in a hypothesis upon which the second year's work is based, but the second year's work often wipes out the first year's hypothesis. If however under compulsion of justification a man has tied himself to his first year's hypothesis and promised results, there is much danger that the rest of the work is forced to conform to the initial misconception.

The control of fundamental research must be in the hands of some University or some kindred body which exempts the scientific man from non-technical criticism. Such a control must impose its own criticism, but this is informed and does not demand immediate results. The government department merely allocates to the research institutions certain monies and only asks a receipt to show that these have been spent properly. It is merely a cash transaction which produces a voucher which may be shown to auditors.

In the second place the staff of a government department is graded and there are heads who are responsible for official views which must be respected. There is no opening for destructive criticism by the lower grades. Given the right personal spirit such criticism may be welcomed, but unfortunately this is not always the case, and the official view stands damning the spirit of investigation. The attitude of the young investigator must be a purely anarchical one, one of disbelief in all things and without trust in accepted views. Such spirit has no place in the rigidity of a government department and the application of a departmental organisation to a Research Institute results in difficulties. We may remember how long the official view of the Geological Department of Scotland regarding the structure of the Highlands was held after it had been renounced by almost the entire body of the Geologists outside.

We may therefore distinguish free research, the hunt for knowledge, under the supervision of Universities or kindred bodies, and administrative research in the laboratories of government departments and by government officials who accept the necessary irksome conditions, such as sudden calls to abandon their particular problem in emergency situations. Even in free research however there must be a certain supervision of expenditure involving inspection which should be generous and enlightened. But there must come a point when the state department makes up its accounts and pronounces whether it is worth while going on with the job. Again the demarcation between departmental and free research has to be left somewhat vague and there must be a frank and generous give and take between them.

The worker in the government laboratories should similarly be given as free a hand as possible. For example many regulations laid down by the administrator involve critical methods and these need investigation, work which may carry a researcher far into the field of problems having little apparent value of direct economic end. Such an overlapping may lead to a danger that claims may be staked out and this must be watched with discretion. When one considers however the small amount of research that has as yet been accomplished and the wide scope offered by agriculture, any serious waste of energy by overlapping is no great danger in this country. And besides a certain overlapping is the lifeblood of investigation, giving that strenuous opposition and real criticism which is so valuable.

Thirdly there is the organisation of research. War time experience has shown that a very great deal can be done by organisation, by the mapping out of the field of investigation and the concentration of many workers upon particular aspects of single problems. Such team work has produced much that is new in medicine. An individual or a committee states the problem and bacteriologist, pathologist, parasitologist all work to a common end. The central body receives reports, calling conferences or interviewing individual workers, making sure that people stick to their texts and finally synthesising the results. It has been suggested that the government should apply the team method to agricultural research and be itself the central coordinating synthesising agent. That the government should organise all the workers as its team, should allocate grants and problems, and gather together the results for direct economic purposes, thus eliminating waste of energy and indeterminate research merely wasting public funds. This is a specious scheme immensely attractive to administrators.

But the analogy with medical research is very imperfect. In medicine there are a very large number of workers who have advanced to the confines of knowledge. There is much material and many laboratories at their disposal, medical schools and hospitals. Further they deal with only one organism, the human being, when the individual is so valuable that great sums may be spent on investigation. But our field presents very different features and there are so few workers that the suggested team work and method of coordination are largely superfluous. Further there is not one but many sciences each equal to human medicine—animal or plant pathology, horticulture, breeding, chemistry and study of the soil, mechanical appliances and so forth, and these are too divergent for coordination to a common end. In fact team work in this realm is largely an illusion.

There are however occasions on which team work would be possible and expedient. For instance during the war it became clear from the results of scientific experiment that the later stages in the feeding of cattle were uneconomic. Yet these results were not acted upon by the farming community for the farmers were not convinced, chiefly because the results had not sufficient volume of evidence and experiment behind them. The only effective way to obtain such evidence would have been to repeat the experiments on a very much larger scale and this could only have been done by allocating the work among various institutions.

Let us turn now to the organisation proposed by the Ministry of Agriculture in dealing with plant diseases and I may say that we are hoping in the next few years to make great advances in this direction. There are still however many financial difficulties, for government grants which at first sight seem liberal compared with those given in the past turn out to be very inadequate when viewed by present day standards.

The following are the various organisations proposed by the Ministry:

(1) *Institutes*, governed by universities or bodies like the Lawes

Agricultural Trust, secure in their independence and free from government control and devoted entirely to *free* research. The state will provide the funds and of course inspect to see that the funds are spent properly.

(2) *Departmental Investigation.* Administrative research carried out by the Ministry's staff of advisers and inspectors, but never becoming a centre of fundamental research into plant pathology. For example one may compare the Ministry's veterinary laboratory at Byfleet with the proposed institute of animal pathology sketched in the Report of the Development Commission. Again, the Ministry's laboratory for administrative research in plant pathology has been placed in Harpenden in order that it may be in the closest possible touch with the free research institute under the Lawes Trust. Attached to the Ministry's laboratory there will be a flying corps of investigators who may be detailed for emergency purposes such as sudden epidemics; these will live with the disease, for successful action depends on close continuous watching. They will require a mobile equipment in order to work on the spot.

(3) *Local Investigators.* It is intended that the staffs of local investigators attached to agricultural colleges shall be strengthened and means will be devised to bring these local workers into close contact with the headquarters staff. In this connection there will be erected advisory councils comprising administrative officers, free research workers and local investigators and it is for these bodies to ensure diffusion of knowledge and combined attack in the face of emergency problems or those which may give scope for team work. There will be no compulsory or official connection between these types of workers, but only their sense of the value of cooperation, which it is hoped will be such as to build up an organisation wherein all the parts are in intimate working relationship.

(4) *Funds.* Finally it may be stated that the Development Commission has funds with which to aid individual workers where necessity arises. Unfortunately there is still a tendency for applications to be made in cases where workers are merely carrying out routine investigations from which it is obvious that little or nothing of value can come. The only remedy for this is to ensure that better men are attracted to this work and for some time this has been a chief preoccupation of the Ministry. It is hoped that this problem has been solved now that a reasonable career can be guaranteed to every man taking up such investigations. This career may not perhaps compete financially with careers in other professions, but it will be a reasonable reward and such only is desired by those who have true research at heart.

II. THE TRAINING PROBLEM.

By Professor V. H. BLACKMAN, Sc.D., F.R.S.,

Professor of Plant Physiology and Pathology in the Imperial College of Science and Technology.

On the principle that one must first catch one's student before one can train him it is clear that the prospects and conditions of service in applied mycological research must be such as to attract students possessing the right qualities. Fortunately conditions in this respect are now much more favourable than they used to be. Advance in the fundamental knowledge which is the pre-requisite to rapid advance in practice can only be attained by workers of high scientific calibre. As the type of training given must bear some relation to the lines on which it is expected that mycological research will advance, I can hardly help touching on fields other than training.

A wide outlook by the student is absolutely necessary, for plant pathology touches botanical science at so many points. Early specialisation must be determinedly avoided. A general training in botany with associated sciences such as is found in most university courses must be the basis of work. This should be followed by special training in systematic mycology, special mycological technique, and plant pathology. Although the student must have a knowledge of the chief groups of fungi, it is impossible in my opinion that all plant pathologists should, as I believe it has been suggested, be competent fungal systematists. The time required to produce such a systematist is far too great, and in general such a proficiency could only be attained at the expense of a knowledge of other sides of the subject.

The number of plant diseases is so large that a student during his training cannot become acquainted with all of them. The most satisfactory way is for the student to gain a first hand knowledge of some of the important diseases in each of the chief groups of fungi, and at the same time to acquire such facility in the examination of diseased plants as will enable him to determine exactly, or approximately, the causal organism or will enable him to isolate the organism for future observation. I may perhaps be forgiven for pointing out, what is really a commonplace

—that in the matter of the determination of the nature of a disease the plant pathologist is in a more difficult position than the ordinary medical man. The doctor attending a human patient is usually able—as the result of a few questions and the observation of symptoms—to state in a few minutes the nature of the disease; it is only rarely necessary to await the discovery of the causal organism before diagnosing the case. This is of course due to the fact that the symptoms of different diseases are, usually, sharply marked in the higher animals. Many diseases of man were quite sharply characterised before the germ theory of disease arose, and to this day the germs of many infectious diseases of man are quite unknown. In plants on the other hand the symptoms are so generalised—that is, common to so many different diseases—that a disease can rarely be determined from symptoms alone. A search has to be made for the causal organism, and when it is found it may have to be grown in artificial culture so that the reproductive organs can be obtained and the nature of the organism established. Days or weeks may thus elapse before the causal organism is identified and the nature of the disease determined.

As however the diseased condition which arises is due to the interaction of the physiological processes of the host and parasite the symptoms of each disease must be different, just as the structure of the gall is different for each combination of host and insect. The trouble is that at present our methods of analysis are not fine enough, so that these symptoms escape observation. We must however look forward to the time when better developed methods of micro-analysis will enable us to classify plant diseases by their symptoms. I may be allowed this digression to indicate the importance of the physiological aspect of plant pathology.

To return to the question of training. What is more important than a knowledge of a large number of diseases is the acquaintance with the sources of information, *i.e.*, books and scientific journals, so that the student may find his way about the subject and have confidence in his power to "get up" any branch of his subject or the knowledge of any special disease.

Since in so many cases insects play a large part in the dissemination of plant diseases some acquaintance with entomology, or at least with the habits of insects which attack plants, is of great advantage. It is clear, however, that it is practically impossible to combine in the same individual a competent knowledge of mycology and a competent knowledge of entomology.

As the questions of immunity bulk so largely at the present day some knowledge of the chief results in this relation of medical bacteriology is valuable, though I for one do not hold the view that the knowledge of toxins or anti-toxins, of lysins, precipitins, and agglutinins, knowledge which has been derived from the specialised study of medical bacteriologists, is likely to give us new weapons in the attack on economic problems of plant pathology.

The days when the only weapons for dealing with plant disease were the tracing of the life-history and the destruction of the parasite at some point in its life-cycle or the prevention of infection by sprays, are now fortunately past, since in many cases the fungus cannot at present be destroyed and the use of sprays is very often impossible. The importance of immune and resistant varieties has come to the front and it has been found that such varieties can be bred or selected. The student of mycology who is to undertake investigation of practical importance must therefore have a knowledge of the results which have been obtained in this direction. One man, however, cannot combine the capacities of a plant pathologist and a plant breeder as has, I know, been expected in some of our tropical dependencies. The two workers must unite their forces and make a combined attack.

I come now to the question of the physiological aspects. Disease is abnormal physiology, so the physiological outlook is a very necessary one, and I am glad to see that the importance of this aspect has been stressed by both Dr Russell and Mr Chittenden. It has long been recognised that the environmental conditions have a marked influence on infection; this they do by affecting the physiological reactions of both host and parasite. The physiological conditions for infection and the physiological processes connected with it are a field of work in which our knowledge is still only just beginning. The fact that different kinds of manuring may markedly affect the degree of infection, and that changes of climatic conditions may even affect the development of a fungus already within the host, show clearly the importance of the physiological aspects of plant pathology. Another question of fundamental importance in plant pathology is that of the physiological differences between immune and susceptible hosts. Also the growing importance of what may be called plant hygiene in reducing the incidence of disease shows the importance in plant pathology of the physiological conditions of the host plant. It is clear from this that the student requires a knowledge of the outlook of modern plant physiology, and therefore some training in modern plant physiology is necessary, and this of course necessitates a grounding in physics and chemistry. No attempt should be made to make of the mycologist a competent physiologist, but such training must be given as will enable the student to appreciate the physiological outlook and to co-operate with the plant physiologist.

The training of the student should include field work even before he specialises in mycology. Ordinary botanical training with its teaching by types and its broad generalisations accentuates the similarities of plants and minimises their differences. Field work corrects this view, to which all of us are prone owing to the psychological desire for simplification; for it brings home the marked differences, not only morphological but physiological, between one plant and another. In the actual mycological training there should be as much acquaintance with disease in the field as is practically possible.

Finally one may point out that a plant pathological problem has usually such wide scientific implications that commonly no one man can hope to solve a problem unaided. For the control of disease the combined attack of the mycologist, plant physiologist and plant breeder is required, in other words, team work, as the Americans call it, is essential.

Finally I would repeat that if mycological research is to develop along lines which will be of the greatest value in practice the investigator must be a man of wide outlook, one who not only will know when to call in the plant breeder and the plant physiologist but also will be able to appreciate their point of view and to combine with them in an attack on the problems of economic plant pathology.

III. THE AGRICULTURAL PROBLEM.

By E. J. RUSSELL, D.Sc., F.R.S.,

Director of the Rothamsted Experimental Station.

In attempting to integrate mycological research with agriculture the great need of the present time is to study the growing plant in the field in health and in disease, both states being regarded as the resultant of the prevailing conditions. The problem falls naturally into two parts which may be labelled the scientific and the practical, the broad distinction being that the practical problem is one for which on grounds of expediency a working solution has rapidly to be found, while the scientific problem though of equal or greater fundamental importance is subject to no such necessity and can be studied at leisure.

The scientific problem is largely one of response. Within certain limits agricultural plants are fairly plastic: by altering easily controlled external conditions wheat plants in one and the same field may be induced to send up 8 or 10 stout stalks bearing ears well set with corn; or on the other hand, only one or two stalks carrying fewer grains. They may be made to form large broad leaves distinctly susceptible to the attacks of rust, or somewhat smaller leaves less susceptible. This is well shown on the Broadbalk wheat field at Rothamsted where there are a number of plots over which the conditions are uniform excepting only in regard to one factor, the nutritive treatment, which varies from plot to plot. The experiment is continued year after year without modification so as to ensure as high a degree of accuracy as is possible. The differences in the characters of the various crops are very clear and sharply correlated with the differences in treatment: the withholding of potash, for instance, is accompanied by marked susceptibility to adverse conditions and to rust attacks. Similarly a field of mangolds (Barnfield) is divided up chess-board fashion into a number of plots on which notable differences in size, vigour, habit of growth and susceptibility to disease are induced by alterations in the soil conditions.

In the mycological problem three sets of factors are involved: the crop, the parasite, and the external conditions. External conditions can again be subdivided into soil and climatic conditions. At Rothamsted an attempt is being made to attack the problem on the following lines. The soil is being studied from the points of view of the chemist, the physicist, and the biologist; under the last heading separate investigators have charge of bacteria, protozoa, fungi, algae, and helminths. The climatic conditions are difficult to study, but a start has been made by following up the work of Hooker at the Meteorological Office, who has indicated certain correlations between weather and crop yields and shown that the subject is susceptible of investigation. As regards methods, one of the chief necessities is the collection and interpretation of data. Here one is met by the special difficulty that there can be no clear cut start. A chemist in securing data can at any time begin anew with perfectly clean apparatus and recrystallised initial substances, whereas in agriculture there is always a previous history to take into account: the composition of the seed is affected by the state of the parent plant, and soil may show the result of treatment after the lapse of many years. One of the plots at Rothamsted is still affected by manurial dressings which were discontinued in 1870. An experiment therefore is only valid when it is done on fields of known history.

But this does not end the difficulties. Scientific investigators are brought up on the Baconian method in which all factors are kept constant except the one under investigation. This method has led to wonderful achievements in the laboratory and is insensibly adopted by workers in all branches of science. In field experiments in our uncontrollable climate, however, it cannot be strictly applied. It is true that two plots may be laid out on which all humanly executed processes such as cultivations and other treatments may be uniform with only one factor, *e.g.* the supply of a particular fertiliser, deliberately varied. But the phenomena shown by the plant are not necessarily effects of this one factor: they may be caused by a totally different factor which has resulted from the interactions of the factor under experiment with some set of soil or climatic factors adventitiously coming together perhaps for the first and last time. Fortunately within recent years a method has been evolved for dealing with cases where several factors vary simultaneously. This is the correlation method, but its application involves the use of mathematics beyond the equipment of the average scientific investigator. The method also requires considerable masses of data.

At Rothamsted the data are all examined by a competent statistician who works out the correlations between the observed effects and the various factors concerned. His results are expressed in curves or in constants: they require for their interpretation detailed study by a competent physiologist who will watch the plants growing in the fields. Remarkably little attention has been devoted to the growth of the plant under natural conditions. A very fruitful field of investigation is opened up by the bringing together at Rothamsted of the statistician, the mycologist, and the physiologist whom we hope shortly to bring into our circle.

A serious difficulty in agricultural investigations is the education of the workers. For convenience of University organisation the realm of Nature is divided up into certain limited areas which we have labelled chemistry, botany, physics, etc., and have come to regard as in some way different things. But the lines are in us and not in Nature. A man dealing with an agricultural problem cannot remain bound by these divisions but must be able to look over the field and see it as a whole. In practice of course this implies a body of men meeting to discuss the problem, and this necessity furnishes the best argument for large central experimental stations which otherwise are open to serious objection. At Rothamsted the staff meetings held every fourteen days to discuss the work prove of great value.

The practical problem differs in several ways from the scientific problem but especially in the degree of urgency. The investigator is asked what he can do to save a particular crop: he must therefore find a solution quickly if he is to afford any help at all. Further, there is an economic factor from which the operations of the medical investigator are entirely free. A grower fixes tolerably sharp limits beyond which he is not prepared to pay for cures for crop diseases.

Experience at Rothamsted shows that the investigation of practical problems is best made at smaller sub-stations set up in the midst of a group of growers particularly concerned. In that way workers specially interested in practical applications can obtain abundant scope for their activities both in supply of material and opportunities for experiment. The central research station gains because it is relieved of work for which it lacks special equipment, thus allowing greater concentration on fundamental problems; it further gains enormously because deductions from the results of its investigations can be tested on a larger scale under different conditions by friendly and perhaps rather candid critics. The close association between Rothamsted and its daughter-station in the Lea Valley is of great advantage to the workers on fundamental problems at Rothamsted. This station was set up to study the problems of the intensive grower under glass, largely producing tomatoes and cucumbers. General principles are taken from Rothamsted or elsewhere, deductions are made bearing on the particular problems of the growers, and then tested on the large scale. The management is vested in a joint committee of scientific men and practical growers, the former being responsible for the programme and the latter for the finance. A mycologist, an entomologist, and an advisory officer have all been appointed: these are all good posts such as any young investigator could accept without loss of self respect.

There is a new spirit abroad among farmers and growers which is of happy augury for the future: it invites cooperation and welcomes the aid of science: nor does it wish only to receive; it is prepared to help scientific work in any way within its power. But as the farmer is often inarticulate it becomes the business of the workers at the sub-station or in the county area to state his problems for him and if possible to put them into such form that they can be investigated. Unfortunately problems in agricultural science are complicated by the multiplicity of the interacting factors; for this reason they are rarely susceptible of the clear cut statement dear to the heart of the pure research worker.

The practical problems in plant disease differ sharply from those presented to the horticulturist and the human doctor; the farmer's plants are so numerous that he cannot hope to give them individual attention but can only treat them in the mass. The elucidation of the phenomena of disease resistance, the study of the effect of environmental factors, and the breeding of resistant varieties, form the best avenues for approaching these problems. In essential principles the work has more in common with that done among human beings on Public Health and Eugenics than with curative medicine. The ultimate aim should be the avoidance of disease.

IV. THE HORTICULTURAL PROBLEM.

By F. J. CHITTENDEN, F.L.S., V.M.H.,

Director of the Royal Horticultural Society's Gardens.

The subject to which I have to address myself is the method by which the results of research into the causation and treatment of plant pathology may be built into general horticultural practice, where the attacks of bacteria and fungi upon cultivated plants growing under horticultural conditions are concerned.

In considering such a subject the mind naturally turns to a survey of earlier attempts in this direction, and seizes upon what appear to be causes of partial failure in the past; and it is largely upon this survey that the remarks that follow are based.

Both Professor Blackman and Dr Russell have traversed parts of the ground which a full treatment of my subject should cover and it is therefore unnecessary to enlarge upon points they have dealt with.

In preparing their campaign of integration mycologists must remember that the problems involved are not only mycological, *i.e.*, belonging to an intimate study of the organisms involved. This study cannot be too intimate and thorough, and it must include an enquiry into the powers of adaptability possessed by the parasite, and also into the range of variation existing or potential within its specific limits. Besides this, the nature of the pathological conditions set up in the host call for study. Further, as is well known, the incidence of disease in plants is dependent to a great extent upon the temporary or permanent environment of the crop, using the term environment in its largest sense. Before mycological results can be thoroughly relied upon, the conditions that favour, as well as those that discourage, the attack of the parasite upon the host must be known, and the range of variation in susceptibility to attack must be studied. Even with the commonest diseases of plants our knowledge is only partial at present, and it would tax the powers of most mycologists to the breaking point if they were called upon to say whether such and such a method of apple-growing would, with absolute certainty, avoid the incidence of even so well known a disease as the common "canker." They could more easily say what would conduce to the attack.

The special problems of the mycologist are, therefore, part only of the matter. The study of plant diseases in its entirety belongs really to the realms of the plant-physiologist, and he may better call to his aid the mycologist to make a special study of the parasite, and the student of plant-relationships and plant-breeding, than that the mycologist should call in the aid of the physiologist. The physiological is the larger problem, and the mycologist should look upon his special task as a branch of the physiological problem. He should, indeed, view his task from the physiological standpoint, and base his work upon a thorough knowledge of physiology.

It is clear that even so far (and this is not all) the problem is one that calls for team work, for no one man can hope to tackle by himself all sides of the problems involved, though one man here and there may be able to co-ordinate the results of all the many lines of work that need to be followed up.

The points so far touched upon are general but there are some special to horticulture, and they on the one hand help to minimize the special difficulties of that art and on the other to increase them. The conditions of cultivation in the garden are, on the whole, more under control, and more artificial (in the sense that they are more "made") than in agriculture or forestry. They are therefore more capable of modification than are those of the field or the forest. The horticulturist aims to secure very large returns from a given area as compared with the agriculturist: his methods are intensive. Furthermore the agriculturist grows only a few adaptable kinds of plants and these in great numbers, while the horticulturist grows many kinds and necessarily attaches great importance to the well-being of every individual; many of these kinds, too, are of limited adaptability. The horticulturist's work entails the frequent removal of growing plants from place to place, sometimes over long distances, and thus increases the danger of carrying disease from place to place. The guarding against the contraction of disease is not so dependent upon one individual's efforts as in agriculture—it is dependent upon the vigilance of several independent persons and the dangers are therefore multiplied.

The task before the individual who attempts to integrate the results of mycological research with horticultural practice are therefore, in any particular case, on the one hand easier and on the other more difficult than in agriculture. He must devise methods of avoidance or of securing absolute immunity which all concerned may be able to adopt, or of preventing attack in the presence of danger, or of lessening the damage in the case of an attack; and in addition he must bear in mind that the treatment must be economical and such as the crop will bear. That is to say, the cost of treatment must be such that the increase in value of the crop resulting will more than balance the extra outlay.

The condition of knowledge in the country among the general public, and even among those who may be reckoned his special clientele, being what it is, he has also at times to awaken the horticulturist to a sense of danger and of loss likely to follow neglect of disease in crops, and this not only on the particular grower's own account but also on account of other persons engaged in similar industries; further he will often have to overcome prejudice as well as inertia in the direction of securing the adoption of the necessary measures of control.

It is clear that to secure these ends the man best fitted for the work will be one who can secure the confidence of practical horticulturists. Comparatively few of the latter can be expected to have either time or opportunity thoroughly to study plant diseases and their treatment; their business is mainly with the art and craft of horticulture—the growing and use of plants for their several purposes. Means to the integration may, however, be found by personal contact between the researchers and the growers. This is the best method and the researcher into avowed practical problems who takes no part in education is apt to become as barren as the teacher who takes no part in or note of current investigation. The widest public can be reached by writing in accessible periodicals or by popular books, but the writing must be clear and in simple straightforward English. The use of technical terms should be reduced to a minimum, but not avoided at the expense of accuracy, and it must be kept clearly in mind that the public whom it is desired to reach have had, as a rule, no opportunity of attaining even the rudiments of the special knowledge which the writer possesses.

Many of the leaflets published from time to time appear to fall short of their purpose because they are written to serve more purposes than one. For these, which are to go to the purely practical man who may be entirely ignorant—and it is to be borne in mind that the troubles of the allotment gardener's cabbage patch are as serious to him as are those of the apple orchard to the fruit-grower—a plain statement of the symptoms of a disease and of the methods of prevention and control is all that is desirable. Those who wish to know more may with advantage be referred to fuller papers. Argument in such leaflets is out of place and technicalities should be strenuously avoided.

Legislative measures may be used as an educative force and so used are likely to have greater value than when made the cloak for protection. And last, but by no means least, demonstration gardens accessible to all, where approved preventive and remedial measures may be seen in operation, will have an enormous influence in effecting the purpose which is the *raison d'être* of this Conference.

V. THE FORESTRY PROBLEM.

BY PROFESSOR W. SOMERVILLE, M.A., D.SC., D.ŒC.,

Sibthorpian Professor of Rural Economy, Oxford.

I UNDERSTAND that the object of this Conference is to attempt to effect an improvement in the co-relation between research and practice, and that my part in the programme is to examine the subject in its relation to Forestry.

The first reflection that occurs to me is this, that while Forestry, Horticulture and Agriculture are essentially alike in principle, in so far that all are immediately concerned with the conversion of air, soil and water into vegetable products, forestry differs from the others in these respects, (*a*) that its returns are long-deferred, (*b*) that the annual value of its out-put per acre is relatively small, (*c*) that its operations are conducted in less accessible areas, and (*d*) that its crop (trees) is physically less amenable to prophylactic or curative treatment and control. To illustrate the last point, let us compare a typical disease of a crop in field or garden, say Finger and Toe, with such a disease of trees as *Chrysomyxa abietis.* I do not say we know all about Finger and Toe, but we seem to know enough about it for all practical purposes. It can be prevented (*a*) by the avoidance of the infection of fresh areas through the agency of parts of diseased plants, including contaminated manure and soil, (*b*) by attention to cultural details, (*c*) by the use of an antiseptic substance such as lime, and (*d*) by the cultivation of resistant varieties of particular cruciferous crops. But in the presence of *Chrysomyxa abietis* one feels almost helpless. If one may take the order of its records as an indication of its progress in this country, it seems to have started in the valley of the Dee in Aberdeenshire, from which it spread into Kincardineshire, then it appeared in Perthshire, and more recently it has been recorded in Northumberland. I do not suggest that the spread of this disease is likely to threaten the spruce with destruction, though, through loss of foliage, trees that are attacked do suffer in growth and may succumb. I only mention it as an instance of a forest-tree disease which some ten years ago, so far as we know, was confined to a limited area, from which it has spread over a wide stretch of country, and in the presence of which we seem helpless to apply preventive measures. All trees subjected to infection do not in this case contract the disease, nor do they in respect of larch disease, *Nectria cinnabarina*, *Melampsorella caryophyllacearum* and other leaf and stem parasites which could be mentioned. Evidently, therefore, there are immune strains amongst the host-plants of certain tree fungi, which suggests the idea of attempting to raise resistant varieties by the application of the laws of breeding which have given good results, with the promise of even better, in the case of field and garden crops. But, here again, we are up against not a fundamental but the practical difference between trees and other crop-plants, namely, that in the latter the period of seed to seed—a generation—is often but a year, whereas in the former it is seldom less than a quarter of a century. Then, again, in the case of at least one highly important field and garden crop—the potato—having raised your immune variety from seed you have the prospect of a commensurable return through years of vegetative reproduction. Although such propagation is not unknown in forest practice (*e.g.* willows and poplars, to some extent limes and elms) it is excluded in the case of most forest trees, which either fail to strike as cuttings, or are hard and costly to propagate as layers, and, at the best, turn out to be mis-shapen undersized individuals. But something can certainly be done in this direction by the exercise of scrupulous care in selecting sound individuals as seed-yielding plants, in the hope that immunity may be a Mendelian character, and that the particular plant may be a homozygote, and that all or most of its ovules may have been fertilised by the pollen of a similar individual. And not only should the seed-collector keep predisposition to disease in view, but other undesirable characters are also transmissible by inheritance, such as feeble growth, twisted fibre, crooked and gnarled stems, and excessive tendency to produce branches, with the consequent result of knotty and inferior timber. These characters are latent in the germ cell. When one sows a batch of tree seed in a nursery, one has the experience of finding that, in say four years, a proportion of the plants are much taller, and a proportion much dwarfer, than the others, and one might be inclined to conclude that this state of things was the result of the external conditions of growth on the particular individuals. No doubt this cause can operate, but it is much less influential than has been supposed. In point of fact it has been proved that the cell elements of dwarf individuals are shorter than those of robust growth, and that the quality of vigour is innate, and is probably a Mendelian character. The question has an important bearing on economic forestry, inasmuch as it is a great mistake to purchase plants by size rather than by age. It is also an advantage to stock an area with many more trees than can find room in even early middle life, for thereby one has the opportunity of selecting robust individuals to stand for the final crop, and in this way the financial returns are much improved. Even in respect of improvement by accidental or deliberate breeding, there is the great difference between agriculture and forestry, in that whereas agricultural plants are, with hardly an exception, hermaphrodites, trees are with few exceptions unisexual. Self-fertilisation, with the opportunity it gives of perpetuating pure strains, while the rule in agricultural crops, is comparatively rare in trees. It is impossible in Salix and Populus, and more or less of an accident in the case of such important genera as Quercus, Pinus, Picea, Larix, Abies, and many others.

While impressed with the special difficulties of Research in forest mycology I am far from suggesting that there are not many hopeful lines that may be pursued. Take, for instance, that most serious pest *Peridermium Strobi.* I will not dwell upon its easily avoidable introduction to North America, where it is threatening the existence of the most important single lumber species of the North American continent, the White or Weymouth Pine. But even in this country its biology is something of a mystery. Its Cronartium stage on Ribes is supposed to be dependent on fresh annual infection with aecidiospores produced by the Weymouth Pine, and yet we are assured by competent observers that in the East of England this Rust occurs abundantly on currant bushes many miles removed from the opportunity of aecidial infection. The question one would like answered is this, is such infection actually produced by aecidiospores, borne by the wind or in some other way, or is it due to uredospores hibernating in fallen leaves? I know of no analogy in support of the latter suggestion, for although Rust of wheat can exist away from the Barberry, it seems to be proved that in this case the uredo stage survives the period between one crop and the next on what the Americans call "volunteer" plants, which are usually not difficult to find in neglected corners, on manure heaps, and in other places. Then, again, in America it has been observed that outbreaks of the aecidial stage occur sporadically many miles away from the infected Ribes, and it is suggested that the sporidia or, it may be, the teleutospores are borne on the bodies of caterpillars of the Gypsy Moth, which are said to be wind-borne over long distances. But the difficulty is to reconcile this statement with the fact that in Bagley Wood near Oxford there is a plantation of Weymouth pines whose North margin comes close up to a cottage garden which contains Ribes. Practically all pines in the outer row close to the garden are infected, but directly you get into the wood even for 10 yards the disease is visibly less frequent, while 100 yards away there is no infection at all. The occurrence of the disease on the Pines is here evidently dependent not only on proximity, but on very close proximity to the teleuto host, and yet teleutospores or their sporidia, one would think, must be easily carried by wind, insects, or birds over the 100 yards of intervening space, much more easily in fact than would be the transference of aecidiospores across miles of country in East Anglia. As a matter of fact Brefeld gives 1–2 days as the usual duration of vitality in the case of aecidiospores, whereas teleutospores, as a rule, pass the whole winter as such and germinate in the following spring. It is the teleutospores, therefore, rather than the aecidiospores, that one would expect to be capable of withstanding the vicissitudes of a long passage through the air, and yet this conclusion does not seem to be supported by experience.

The integration of research, mycological and other, with the practice of forestry may be regarded from several points of view. There is, first of all, the question as to the relationship of research to practice. It is only when such relationship is aggressively obvious that some people take an interest in research at all. If only research is to be undertaken whose practical bearings are at once self-evident, then we may say good-bye to all progress of the type which persists and endures. It is a mere platitude to say that some of the biggest advances in industrial methods have emerged as side-issues in purely theoretical investigations. Do not therefore let us discourage research, for instance, into the constitution of the cell-wall; it may perhaps unexpectedly throw light on methods of impregnation with preservative materials, a subject of great and growing importance in view of the diminishing supplies of timber. Or, again, the forester does not take much interest in the initial stages of a research which may be concerned with the technical details of the hybridisation of two species of poplar, but he is not slow to appreciate the results when he is presented with a new variety which gives him a volume-yield per acre 50 per cent. greater than he has ever known before.

Another aspect of the subject is concerned with diffusion of knowledge —the bringing home to the practitioner of the results of scientific teaching and research. This is a difficulty in all industries, but particularly in forestry. In a large industrial concern there are always men associated with the management who are quick to appreciate suggestions, and who have the opportunity to test them in practice. Even in agriculture the farmer has the power to reorganise his rotations and cultivations, to test new crops or new varieties of crop plants, to secure new manures or to revise his manurial system. In the case of the forester the situation is somewhat different. He is slow to change his methods because he is dealing with a crop which may not mature for a century, and a mistake on his part cannot be corrected in a year or two. Moreover, he is rarely in a position of sufficient independence to have the power to adopt drastic modifications even were he qualified by training to make large decisions. It is really the owner who should be educated in scientific methods so that he may intelligently direct the management of his woodlands. There is no doubt that a great change for the better has, during the past 20 years, come over the outlook of many estate owners in respect of their woodlands. This body may still be small and select, but it will grow, and it contains men of quick intelligence who are keen and alert to appreciate all that science can show them. At the moment we are at the parting of the ways in respect of forestry. We are witnessing the break-up of large estates, and the passing of much of the land, including woodlands, into the hands of smaller owners. Judging by what has happened in Ireland under somewhat similar circumstances the new owners, many of them farmers, are not likely to take much interest in their plantations except in so far as they can be converted into cash. But simultaneously with this change of ownership we have seen the creation of a Forestry Commission which is charged with the duty of extended afforestation, and the improvement of existing woodlands. I imagine therefore that in the near future we shall see extended provision made for the supply of scientific advice to woodland owners, and probably also schemes of co-partnership between the State and the individual. In this way the relationship between research and practice should be rendered much closer, and, especially so, as the Commission is likely to take steps to encourage, or even directly to undertake, forestal investigation and education. Then, again, the Commission is pledged to acquire large areas of land for fresh afforestation, and the advantages of scientific practice as illustrated in the State forests will react on the management of private areas.

At no time were class rooms and laboratories so crowded with prospective landlords as at present, and it is the general experience that these new students are imbued with an earnestness and keenness that is most stimulating to their teachers. Only a small proportion of them will become investigators in the narrower sense of the term, but all of them it is hoped, will be sufficiently immersed in the scientific atmosphere to know what research means, and to appreciate its bearings on progress in agriculture, horticulture and forestry. The future landowner must take a much closer interest in his land than has generally been the case in the past, and his interest in his woodlands must be economic and scientific rather than hereditary, sporting and aesthetic. Then below the landowner there is the forester, and already, I understand, the attention of the Commission is being directed towards schemes of a thorough-going character for his education. It is, in fact, to the improvement of education all round that we may most hopefully look for enhanced appreciation of science, and when this advance has been secured the integration of research with practice will be a natural and inevitable consequence.

VI. GENERAL DISCUSSION.

Sir David Prain (*Director of the Royal Botanic Gardens, Kew*).

I have been asked to say something about the scope and functions of the Imperial Bureau of Mycology in its relation to the activities of Economic Biologists and to the already existing research institutions. I can only state that in all these things its part will be like that played by the Imperial Bureau of Entomology. As you are aware some ten years ago this Bureau was founded by the Entomological Committee and since that time it has, under the directorship of a member of this Association, developed in a most extraordinary manner. We hope that the Imperial Bureau of Mycology may be equally successful. The intentions underlying its foundation are similar as will be its functions, and we hope that its value to economic biology will be equally great.

E. S. Salmon (*Agricultural College, Wye*).

After listening to the papers which have been delivered this morning, two things will be present in all our minds. The first is the wide scope of economic mycology, and the second the need and value of conferences such as this.

It is interesting to look back on the progress of economic mycology during the last fifteen or twenty years. The practical man has learned how to deal successfully with disease owing largely to descriptions of the fungus and control measures written in simple language. The availability of such technical knowledge to the practical man is very recent, and one may instance the ignorance fifteen years ago of the Kent apple grower regarding Apple Scab. The leaflets published by the Ministry of Agriculture mark a great advance in the diffusion of knowledge and one may now be thankful that these leaflets are safe on the scientific side. The question has been raised whether there should not be two kinds of leaflet, one for the less and one for the better educated grower, but the present issues are certainly not too technical for the farmers and fruit growers of Kent.

Detailed knowledge is essential to practical control of the disease. The life-history of the species is not sufficient, for there are physiological species within the morphological species as in the case of the Monilia causing the Brown Rot of fruit, and investigation of these physiological differences is of the most direct practical importance to growers.

The history of the American Gooseberry Mildew is very interesting from our point of view, for little was done to educate opinion until legislation came into force. The year 1907 was memorable in that the Diseases of Insects and Pests Act then came into force and the working of this Act and the inspection by the Ministry Officials has been of great educational value.

There are certain other steps to which I may refer. At a fruit growers' conference at Wye a fine-spray American nozzle was exhibited and at first one was blamed for introducing "foreign stuff." This pattern was however not patented in this country and commercial makers immediately recognised its value and manufactured copies which are now used widely. There is very much yet to be done in the improving of such mechanical objects and their operation.

I should also like to see travelling scholarships given by the Board so that students could see the best practice in disease control in other countries and bring back first hand knowledge.

Great steps have recently been made regarding the standardisation of fungicides. In 1909 a standard lime sulphur wash was first demonstrated at Wye and since that time has had wide recognition. The value of standardisation is obvious and commercial manufacturers are now themselves demanding that the washes sold should be of guaranteed specific gravity.

I agree with Professor Blackman that the physiological point of view is essential in our subject, but equally imperative is field experience not only of the crops but of the growers. A grower with a diseased plantation may not ask how he shall treat the disease but what will be the effect of pigs on the land. One must not only have a knowledge of fungi but a wide experience of the potentialities of the host plants.

F. T. BROOKS (*Botany School, Cambridge*).

Plant physiology is all important and I should like to spend the next five years in this study and then return to plant pathology. Equally important is field work, for this is widely different from laboratory knowledge. Only in the field can one obtain any true idea of the epidemic spread of disease, of the relative susceptibility of varieties to disease and the fact that environmental conditions often play a more important part than the actual pathogen. A tropical pathologist of acumen suggested that a necessary preliminary to mycological work was the digging of drains and there is much to be said for this. It is essential that the mycologist should have a sympathetic attitude to the cultivator and from his earliest stages contact with growing crops is essential. Intimate crop knowledge is imperative, for too often it is complained that the suggested remedies are worse than the disease. Treatment must be on an economic basis.

The teacher must possess a wide outlook so as to counteract the tendency to segregation of knowledge which up to a point is necessary to progress but dangerous if over-emphasised. There are bound to be the teaching aspect, the research and the advisory branches but the teacher himself must be sufficiently broad to give the students the necessary comprehensive viewpoint. Often in the laboratory there is a false perspective and much time is wasted on labouring trivialities which should be spent on big problems. Only crop and field experience enable one to see things in their right proportions.

A. D. COTTON (*Ministry of Agriculture*).

I have been asked to describe briefly the kind of administrative research which will be carried out in the Ministry's new laboratory at Harpenden, for in future there will be two laboratories situated there, the Institute of Plant Pathology controlled by the Lawes Trustees and the Ministry's laboratory. The functions of the latter may be classified under four headings.

1. *Intelligence.* This mainly concerns the plant disease survey of which one report has already been issued and one is now in the press. This deals with the incidence and relative importance of pests, primarily of agricultural plants but also of those affecting trees and ornamental plants. Full records are kept and these will be available to all interested.

2. *Advisory.* This work entails a great amount of routine correspondence but it is expected that this will be reduced when the new leaflets are widely spread. It will also comprise the exhibition of specimens, field demonstrations and propaganda.

3. *Administration.* This work is often uncongenial to the scientific man but it must be done. The regulations concern the practical grower and they must be issued in consultation with him, the scientific man safeguarding their accuracy to fact. Trade regulations must have the support of the growers.

4. *Research.* Often there are problems of immediate urgency such

as sudden widespread outbreaks of disease and these must be investigated by the Ministry's officers. There is also much research work of a tedious routine nature which must be carried out, such as control methods and spraying problems. The American Gooseberry Mildew for example has been studied for nineteen years and its control is still imperfect. In addition there are always special problems elucidation of which is very desirable and these will not be neglected. To appreciate these special points the workers need to possess the true research spirit.

Professor A. HENRY (*Royal College of Science, Dublin*).

I agree generally with Professor Somerville's remarks. I wish to point out that attacks by fungi on trees in plantations twenty, thirty or more years old may involve greater financial loss than is the case in attacks of fungi on other cultivated plants. The accumulated capital of many years growth of timber may be completely destroyed.

We know that *Pinus stobus* can no longer be cultivated in Europe on account of the destructive effects of blister rust. This fungus, carried into the United States by young trees from German nurseries a few years ago, now threatens the existence of the extensive forests of this valuable pine in the United States. *Thuya gigantea*, a tree hitherto regarded as immune from disease and cultivated considerably in Britain and Ireland, has recently been attacked by a fungus, *Keithia Thujina*, which may spread and render valueless plantations of this species made in the last twenty years. At present afforestation is carried out mainly with exotic species; some like the European larch, hazardous to cultivate on account of the canker which infests it in so many situations; other species, like the Douglas fir and Sitka spruce, up to the present free from disease, and forming the bulk of many new plantations. If disease of a similar character to those first mentioned attacks the two last most valuable trees, say in ten or twenty years time, enormous loss will be incurred by the State and by private owners of woods.

What is wanted is a number of workers in mycology, who will tackle under field conditions the problem of the attacks of fungi on our common forest trees, to refer both to old and well-known enemies like larch canker and *Agaricus melleus* and to new diseases like *Keithia Thujina.*

Afforestation, without concurrent research into disease, may turn out in many cases a disastrous failure.

A. B. Bruce (*Ministry of Agriculture*).

It is essential that the research worker be assured of a reasonable reward and I may perhaps indicate the scheme which has been formulated by the Ministry to improve the prospects of those engaged in investigation. A research service is to be formed analogous to the Civil Service which will provide research scholarships and permanent posts with salaries graded to a maximum of £800 per annum, above which would be the directors of the institutes. Such a rising scale cannot ensure a Newton or a Pasteur but it is a great improvement on past conditions and marks a very definite victory for a state department wrestling with a reluctant Treasury. There is further the guarantee of a pension and it is hoped ultimately to extend such a scheme not only to research institutes obtaining government grants but to advisory workers at agricultural colleges.

The Chairman (Professor F. Keeble) referred to the share Mr Bruce had taken in winning this victory and the debt of gratitude owing to him.

A. B. Bruce (*Ministry of Agriculture*) wished to associate with himself Professor Keeble, Sir Daniel Hall and especially Mr Dale.

H. V. Taylor (*Ministry of Agriculture*).

The first thing the mycologist must do is to study the farmer and grower, for unless he can appreciate their attitude, he is likely to possess but little influence. I should also like to emphasise the value and necessity of team work. For example 100,000 tons of potatoes were rotting in Lincolnshire and the mycologist was called in and found blight. But the matter was not so simple, for the bacteriologist reported bacterial rot following blight. Again the weather was probably much to blame, for the season had been very wet and the crop late and showing second growth, which were physiological and meteorological matters. Team work throwing light on the problem from many aspects is necessary if the farmer is to be advised accurately.

Regarding administrative problems the scientist is apt to overlook just the points which the administrator insists upon and any regulations issued must not only have a scientific basis, but be economically sound and applicable on a practical scale. In my opinion there is little hope for any real progress in mycological applications until satisfactory team work is carried out.

A. B. Lister (*Lea Valley Experimental Station*) spoke as an advisory officer attached to a Research Station rather than as a specialised research worker. Generally speaking the practical man has a certain contempt for the scientific man because in his experience the average scientist knows little of plant culture under commercial conditions. Practical experience is essential. No less important is compatibility of temperament, for growers include all classes of men. An ideal scheme of co-ordinated research would include central stations such as Rothamsted where fundamental principles could be elucidated; then smaller sub-stations such as those in the Lea Valley and at East Malling where particular crop problems could be dealt with. These latter should each have an advisory officer forming a connecting link between the growers and laboratories. Purely administrative officials such as the Ministry's inspector should also be in touch with some central or district laboratory. In the past there has not been sufficient coöperation. The advisory officer is comparable with the medical practitioner who is also medical officer of health for his district, whilst the laboratory is akin to the specialist. The fundamental problem in all advisory work is to gain the confidence of the grower. Having this, experiments can often be carried out in the actual nurseries under the most severe commercial conditions and these are extremely valuable, not only to the particular grower but to the industry as a whole.

G. C. Gough (*Ministry of Agriculture*).

The inspector must learn his facts from the crop, for it is not infrequent that a laboratory recognition of a disease is useless in the field. He must also possess much tact, for practical men are of all manners and conditions and respond very differently. The administrative regulations however apply to all growers and must therefore be simple and straightforward. They must also not be selective but treat all alike and this has sometimes not been the case. It is essential that the formulation of such orders be carried out by scientists in conference with field men, for laboratory truths do not always hold in the field. For example many "new" diseases have been described by scientists but in every case it has been found that these are really of old standing and widespread incidence and that their "introduction" or "newness" is merely due to the fact that they have been overlooked.

W. F. Bewley (*Lea Valley Experimental Station*).

The success in bridging the gap between the central research institute and the grower depends upon the success of the sub-station, and the success of the sub-station depends upon the scientific worker. The success of the mycologist in such work depends upon his skill in experimental technique, his experience and his keenness for work. To this must be added a thorough knowledge and sympathy with practice. The physiological aspect of the work is of great importance and much has yet to be done with plant hygiene. If possible the worker should commence with simple problems which will give "quick" positive results ensuring the confidence of the grower. The personal qualities of the worker are all-important. He must gain the friendship of the growers, exercise much diplomacy, be impervious to the innuendos of doubting members, be extremely careful and not too hasty to advise, and possess a wholesome lack of conceit.

Finally I would emphasise the need for some kind of clearing-house for Government officials, research institutes and sub-stations, some body which would gather together the special information and knowledge possessed by each branch and circulate it for the good of all. The great value of such a conference as this is that it brings together all workers.

Miss D. M. Cayley (*John Innes Horticultural Institute*).

There are many abnormal conditions of plants which while not due to the action of any pathogen are yet from the practical point of view to be regarded as diseases. Such for example are the bolting of turnips, lettuce, cabbages and other plants which are a source of considerable financial loss; or the rogueing of peas and potatoes which occasion the expenditure of valuable time and money. In the elucidation of these problems of plant pathology breeding is of primary importance and the facilities for this type of work are in this country extremely meagre. The value of breeding experiments in the securing of strains immune to fungal and bacterial disease needs no emphasis but it is not always realised that its value does not cease when the immune variety has been obtained. Such plants are often low croppers and the further problem is to raise them by breeding to an economic status.

Dr. J. C. Willis spoke from an experience of twenty years direction of tropical research stations in which the problems of plant disease are ever before one. The crops, such as tea, rubber and coco-nut, are mainly perennial and cannot be handled so easily as the annual crops in English agricultural practice. Further there are no small watertight compartments but extensive areas planted solely to tea, coffee and so forth, and diseases therefore have every opportunity of spreading on an epidemic scale.

The problem of disease control is always an economic one and the skill required is largely that of the handling of men and money. For example many treatments have been suggested for the Coffee Leaf Disease but none which are not too expensive to apply. It is cheaper to let the plant and the disease die out, but this course only serves to spread the disease by providing centres of infection. On the other hand the speaker and Mr E. E. Green had discovered remedial treatment for cocoa canker which being simple and economically sound is extensively applied.

J. R. Ramsbottom (*Natural History Museum*).

The problems of the growing plant and its relation to the environment are questions for the horticulturist and agriculturist. In plant pathology the mycologist must know the fungus and regard the disease as the result of the interaction of the host fungus complex and the environmental conditions. Economic mycology however is inclusive of more than plant disease. There is for example the relation of fungus to host in such plants as the Ericaceae or Orchideae and the problems centering around the mycorrhizal relation are of very great economic importance. There is also the further problem of the fungi present in the soil and the part they play therein.

Questions of plant disease are undoubtedly largely physiological in nature but even a competent physiologist trained in laboratory technique may meet snags in his application of such knowledge to field problems.

Finance must always play a prominent part in plant pathology, for uneconomic remedies are of no use however successful they may be under trial conditions. Finally the plant pathologist must be able to identify the common fungi he meets with and this requires a certain amount of systematic study.

Miss E. M. Wakefield (*Royal Botanic Gardens, Kew*).

The plant pathologist cannot be a competent systematist but he must have sufficient acquaintance with systematic work not only to identify the pathogenic organisms but to recognise new species, and to describe them accurately so that others may recognise them from his diagnoses. Mistakes in identification have been only too frequent and much confusion has resulted.

Dr H. Wormald (*Agricultural College, Wye*).

This conference has shown the great necessity for increasing the number of workers in plant pathology so that our problems may be investigated here. At present we are compelled to rely largely on American and other work not only for the diagnosis of our diseases but for recommendations as to treatment. It must however be recognised clearly that conclusions which hold in other countries do not always apply here and that if we are to obtain accurate solutions of our problems, those problems must be studied in the place where they occur. For example it was believed, accepting Woronin's conclusions, that *Monilia fructigena* was practically confined to apples and pears and *M. cinerea* to stone fruits. It has been shown however that in this country *M. fructigena* may produce cankers on plums and *M. cinerea* a blossom rot of apples. Similarly conclusions arrived at in America cannot be relied upon to hold true for England.

Furthermore cultural methods of investigation have shown that there are different physiological races of *M. cinerea*. Progress in mycology will largely result from the development of cultural laboratory methods.

Dr S. G. Paine (*Imperial College of Science*).

This conference has evolved a very exalted idea of what a mycologist should be and the knowledge he must possess—physics, chemistry, botany, mycology, farming and so forth. Such an ideal is unattainable. There is still however one other subject of which a mycologist should have knowledge and that is bacteriology. Not only is the importance of the bacteria as causal agents of disease in plants being increasingly recognised, but the bacteriological technique is being more and more extensively adopted in experimental mycology. A bacteriological training is largely one in clean cultural method and such training should take an early and important place in the education of every mycologist.

Professor F. Keeble (*Botany School, Oxford*).

We have heard many schemes from people partial to one or another aspect of the problem which has been before us and this conference has been of great value in bringing together and synthesising these schemes.

There must be a directing body, a milch cow providing money. There must be large research institutes carrying out fundamental investigations and radiating from these subsidiary stations situated in commercial growing areas and concerned with the actual crop problems. There must be a light cavalry—advisors who will leave the untrammelled realms of pure research and move rapidly over the field of action. There must be county organisations, technical men who will formulate the problems and ask help in their solution, and these county organisations are an essential part in the whole. This staff of people in intimate contact with the commercial growers will arrange demonstration plots and trial grounds, the county organisation giving the facilities for such local experimentation. Finally the Board of Agriculture will defray expenses on a pound for pound basis. The Board recognises the importance of bringing together the administrator and the research worker and the integration of both research and administration with practice. No scheme can be a final or a permanent one; it will need to be modified, perhaps reversed, but the wider the basis on which it is founded the more stable it will be.

We must recognise the great value of such conferences as this and hope that it may be the precursor of many.

The proceedings closed with a vote of thanks to the Chairman.

LIST OF MEMBERS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS FOR 1920.

1914. Adair, E. W., *Department of Agriculture, Cairo.*
1920. Adams, Miss E. F. M., B.Sc., *Seed Testing Station, Leigham Court Rd., Streatham Hill, London, S.W.*
1908. Alcock, Lt.-Col. A. W., C.I.E., M.B., LL.D., F.R.S., *Heathlands, Belvedere, Kent.*
1914. Anstead, R. D., *United Planters' Association, Bangalore, Southern India.*
1908. Ashworth, Prof. J. H., D.Sc., F.Z.S., 69, *Braid Avenue, Edinburgh.*
1914. Awati, P. R., *Central Research Institute, Kasauli, India.*
1920. Bacot, A. W., *Lister Institute, Chelsea Gardens, London, S.W.* 1.
1914. Bailey, M. A., 49, *Alleyn Park, Dulwich.*
1905. Balfour, Andrew, C.M.G., M.D., 25–27, *Endsleigh Gardens, London, N.W.* 1.
1914. Ballard, E., F.E.S., *Government Entomologist, Coimbatore, Madras.*
1920. Balls, W. Lawrence, Sc.D., M.A., *Fine Cotton Spinners' Association, St James's Square, Manchester.*
1914. Barker, Prof. B. T. P., M.A., *National Fruit and Cider Institute, Long Ashton, Bristol.*
1920. Bayliss Elliott, Mrs J. S., D.Sc., *Botany School, The University, Birmingham.*
1919. Beer, R., *Westwood, Bickley, Kent.*
1914. Beeson, C. F. C., *Forest Research Institute, Dehra Dun, India.*
1920. Benson, Prof. Margaret, D.Sc., F.L.S., *Botany School, Royal Holloway College, Englefield Green, Surrey.*
Hon. Berlese, Prof. Dr Antonio, *R. Staz. di Entomologia Agraria, Firenze, Italy.*
1919. Bewley, W. F., M.Sc., *Experimental Station, Cheshunt, Herts.*
1915. Bijl, P. A. van der, M.A., F.L.S., *Natal Herbarium, Berea, Durban, S. Africa.*
1914. Billinghurst, H. G., F.R.M.S., 76, *Lebanon Gardens, Wandsworth, S.W.* 18.
1920. Bintner, J., *Helmdange, Grand Duché de Luxembourg.*
1920. Blackman, F. F., M.A., Sc.D., F.R.S., *St John's College, Cambridge.*
1919. Blackman, Prof. V. H., M.A., Sc.D., F.R.S., *Imperial College of Science, S.W.* 7.
1909. Bles, E. J., D.Sc., *Elterholm, Madingley Road, Cambridge.*
1916. Bocock, C. H., F.E.S., *The Elms, Ashley, Newmarket.*
1920. Borthwick, A. W., O.B.E., D.Sc., *Forestry Commission*, 25, *Drumsheugh Gardens, Edinburgh.*
Hon. Bos, Prof. Dr J. Ritzema, *Willie Commelin Scholten, Amsterdam, Netherlands.*
1920. Boycott, Prof. A. E., M.A., D.M., F.R.S., 17, *Loom Lane, Radlett, Herts.*
1920. Brade-Birks, Rev. S. Graham, M.Sc., 16, *Bank St., Darwen, Lancs.*
1919. Brenchley, Miss W., D.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*
1914. Brierley, W. B., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*

1920. Bristol, Miss B. M., D.Sc., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*
1914. Brooks, F. T., M.A., *The Botany School, Cambridge.*
1920. Bruce, A. B., M.A., *Food Production Department, Ministry of Agriculture and Fisheries*, 72, *Victoria Street, London, S.W.* 1.
1920. Buddin, W., M.A., 194, *Balfour Road, Ilford.*
1914. Burns, W., *Office of Economic Botanist, Agricultural College, Poona, India.*
1920. Campbell, A. V., *The Croft, Harpenden, Herts.*
Orig. Carpenter, Prof. G. H., D.Sc., *Royal College of Science, Dublin, Ireland.*
1914. Cayley, Miss D. M., *John Innes Horticultural Institute, Merton, Surrey, S.W.* 19.
1905. Chandler, S. E., D.Sc., *Imperial Institute, London, S.W.* 7.
1919. Chipp, T. F., B.Sc., *Botanical Gardens, Singapore.*
1908. Chittenden, F. J., F.L.S., V.M.H., *The Laboratory, R.H.S. Gardens, Wisley, Surrey.*
Hon. Cholodkovsky, Prof. Dr, M.A., *Institut Forestier, Petrograd, Russia.*
†1905. Cornwallis, F. S. W., *Linton Park, Maidstone, Kent.*
1915. Cotton, A. D., *Pathological Laboratory, Royal Botanic Gardens, Kew.*
1918. Cragg, P. A., *Merivale Nurseries, Heston, Middlesex.*
Hon. Cuboni, Prof. Guiseppe, *Phytopathological Station, Rome.*
1920. Cunliffe, N., *Research Institute, School of Forestry, Oxford.*
1920. Cutler, D. W., M.A., *Rothamsted Experimental Station, Harpenden, Herts.*
1920. Cutting, E. M., M.A., F.L.S., *Botany School, University College, Gower St., London, W.C.* 1.
1920. Darbishire, Prof. O. V., Ph.D., F.L.S., *Botany School, The University, Bristol.*
1920. Davey, Miss A., M.Sc., *Botany School, University College, Bangor.*
1915. Davidson, J., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*
1920. Deacock, R. J., B.Sc., *School House, Crundale, Canterbury.*
1914. Deakin, R. H., *Joan Cottage, Bamford, Derbyshire.*
1920. Delf, E. M., B.A., D.Sc., F.L.S., *Westfield College, Hampstead.*
1915. Doidge, Miss E. M., M.A., F.L.S., *Division of Botany, Dept. of Agriculture, Pretoria, S. Africa.*
1918. Downes, H., M.B., Ch.M., F.L.S., F.G.S., F.R.M.S., *Ditton Lea, Ilminster.*
1920. Drummond, M., M.A., F.L.S., *Botany School, The University, Glasgow.*
1920. Duffield, C. A. W., F.E.S., *Stowting Rectory, Nr Hythe.*
1917. Eltringham, H., M.A., D.Sc., F.E.S., 6, *Museum Road, Oxford.*
1914. Emptage, W. F., 1, *Ullswater Road, West Norwood, London, S.E.* 27.
1916. Eyre, J. A. Vargas, D.Sc., *S.E. Agricultural College, Wye, Kent.*
1909. Farmer, Prof. J. B., D.Sc., F.R.S., *Imperial College of Science, South Kensington, S.W.* 7.
1905. Freeman, W. G., A.R.C.S., B.Sc., *Royal Botanic Gardens, Trinidad.*
1919. Fryer, C. H., 11, *St Mary's Road, Tonbridge, Kent.*
1913. Fryer, J. C. F., M.A., F.E.S., *The Pathological Laboratory, Royal Botanic Gardens, Kew.*
1919. Fryer, P. J., F.I.C., *Ravenscar, Tonbridge, Kent.*
1918. Gahan, C. J., M.A., D.Sc., F.E.S., *British Museum* (*Natural History*), *Cromwell Road, S.W.* 7.

1914. Gamble, Prof. F. W., D.Sc., F.R.S., *The University, Edmund Street, Birmingham.*

1914. Gardiner, Prof. J. S., M.A., F.R.S., *Bredon House, Selwyn Gardens, Cambridge.*

1920. Gates, R. R., B.Sc., Ph.D., F.L.S., *King's College, Strand, London, W.C. 2.*

1920. Glynne, Miss M. D., B.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*

1908. Gough, G. C., B.Sc., 44, *Hazlewell Road, Putney, S.W.*

1914. Gough, L. H., Ph.D., F.E.S., *Agricultural Department, Cairo, Egypt.*

1905. Green, E. E., F.E.S., *Way's End, Camberley, Surrey.*

1909. Groom, Prof. P., M.A., D.Sc., *Imperial College of Science, South Kensington, S.W. 7.*

1915. Gunn, David, *P.O. Box* 1013, *Pretoria, S. Africa.*

1914. Güssow, H. T., F.R.M.S., 43, *Fairmount Avenue, Ottawa, Ontario, Canada.*

1920. Gwynne-Vaughan, Dame Helen, D.B.E., D.Sc., LL.D., F.L.S., *Botanical Department, Birkbeck College, Chancery Lane, London, E.C.*

1909. Hadwen, Seymour, D.V.Sci., *Dominion Experimental Farm, Agassiz, Canada.*

1914. Hamilton, Dr. Lillias, *Agricultural College for Women, Studley.*

1920. Henderson Smith, D. J., M.D., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*

1907. Hewitt, C. G., D.Sc., F.E.S., *Dominion Entomologist, Dept. of Agriculture, Ottawa, Canada.*

1910. Hickson, Prof. S. J., M.A., D.Sc., F.R.S., F.Z.S., *The University, Manchester.*

1920. Hiley, W. E., M.A., *Research Institute, School of Forestry, Oxford.*

1920. Hill, A. W., Sc.D., M.A., F.R.S., F.L.S., *Royal Botanic Gardens, Kew.*

1920. Holden, H. S., M.Sc., F.L.S., *University College, Nottingham.*

Hon. Hopkins, A. D., Ph.D., *Bureau of Entomology, Department of Agriculture, Washington, D.C., U.S.A.*

1919. Horne, A. S., D.Sc., F.L.S., F.G.S., *Imperial College of Science, South Kensington, S.W. 7.*

Hon. Howard, Dr L. O., *Bureau of Entomology, Department of Agriculture, Washington, D.C., U.S.A.*

1920. Hunter, Bernard Keith, *Oldfield, Swanage, Dorset.*

1914. Hutchinson, C. M., *Pusa P.O., Darbhanga District, Bihar, India.*

1914. Hutchinson, H. P., *The Laurels, Kegworth, Derby.*

Orig. Imms, A. D., D.Sc., F.L.S., F.E.S., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*

1920. Isaac, P. V., B.A., F.E.S., 2, *Gledhow Terrace, South Kensington, London, S.W.*

1918. Jackson, Miss D. J., *Swordale, Evanton, Ross-shire.*

1920. Jackson, Miss V. G., B.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*

1918. Jardine, N. K., *Peradeniya, Ceylon.*

1907. Jepson, F. P., *Peradeniya, Ceylon.*

1920. Jewson, Miss S. T., B.Sc., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*

1920. Jones, Prof. W. Neilson, M.A., F.L.S., *Bedford College, Regent's Park, London, N.W.*

1918. Kannan, Kunui, M.A., F.E.S., *Asst. Entomologist, Govt. of Mysore, Bangalore, S. India.*

1915. Keeble, Prof. F., C.B.E., M.A., D.Sc., F.R.S., *Botany School, Oxford.*

1920. Kidd, F., M.A., D.Sc., *Botany School, Cambridge.*

1907. King, H. H., F.L.S., F.E.S., *Gordon College, Khartoum, Sudan.*

1907. King, Prof. L. A. L., M.A., *West of Scotland Agricultural College, Blythswood Square, Glasgow.*

1908. Lees, A. H., B.A., *National Fruit and Cider Institute, Long Ashton, Bristol.*

Orig. Lefroy, Prof. H. Maxwell, *Imperial College of Science, South Kensington, S.W. 7.*

1909. Leigh, H. S., M.Sc., *Brentwood, Worsley, Nr Manchester.*

1909. Leiper, R. T., M.D., D.Sc., 103, *Corringham Road, Golder's Green, N.W.*

1914. Lesley, J. W., *Emmanuel College, Cambridge.*

1915. Lister, A. B., B.Sc., D.I.C., *Experimental Station, Turner's Hill, Cheshunt, Herts.*

1920. Lloyd, Llewellyn, M.Sc., *Experimental Station, Turner's Hill, Cheshunt, Herts.*

†Orig. MacDougall, R. S., M.A., D.Sc., F.R.S.E., F.E.S., 9, *Dryden Place, Edinburgh.*

1914. McClellan, F. C., M.R.A.C., F.L.S., *Director of Agriculture, Zanzibar.*

1920. McLean, Prof. R. C., M.A., D.Sc., F.L.S., *Botany School, University College, Cardiff.*

1920. McLean Thompson, J., M.A., D.Sc., F.R.S.E., *Botany School, Glasgow.*

1909. Mangan, J., M.A., *University College, Galway.*

1920. Mangham, S., M.A., *Botany School, Armstrong College, Newcastle.*

1917. Mann, H. H., D.Sc., F.L.S., *Agricultural College, Poonah, India.*

Hon. Marchal, Prof. P., *Station Entomologique*, 16, *Rue Claude Bernard, Paris.*

1914. Marshall, G. A. K., D.Sc., F.Z.S., F.E.S., 6, *Chester Place, Hyde Park Square, W.; and Imperial Bureau of Entomology, British Museum (Natural History), Cromwell Road, S.W. 7.*

1920. Mason, Francis Archibald, 29, *Frankland Terrace, Leopold Street, Leeds.*

1920. Matthews, Mrs D. J., M.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*

1920. Mellor, J. E. M., B.A., 51, *Onslow Square, London, S.W.* 7.

1914. Moore, Sir F. W., M.A., M.R.I.A., V.M.H., *Botanical Gardens, Glasnevin, Dublin, Ireland.*

1920. Morris, Sir Daniel, K.C.M.G., M.A., D.Sc., LL.D., D.C.L., C.M.Z.S., V.M.H., F.R.H.S., 14, *Crabton Close, Boscombe, Hants.*

1920. Mosley, F. O., F.L.S., *Laboratory of Plant Pathology, University College, Reading.*

1920. Murphy, A. J., 2, *Dorset Square, London, N.W.* 1.

1914. Neave, S. A., M.A., D.Sc., F.Z.S., F.E.S., 24, *De Vere Gardens, Kensington, W.* 8*; and Imperial Bureau of Entomology*, 88, *Queen's Gate, S.W.* 7.

Hon. Neumann, Prof. L. G., *Ecole Nationale Vétérinaire, Toulouse, France.*

Orig. Newstead, Prof. R., M.Sc., F.R.S., A.L.S., *School of Tropical Medicine, The University, Liverpool.*

1918. Olive, G. W., *Grafton House, Oundle, Northants.*

1920. Oliver, Prof. F. W., M.A., D.Sc., F.R.S., *Botanical Department, University College, London, W.C.* 1.

1910. Osborn, Prof. T. G. B., *The University, Adelaide, S. Australia.*
1919. Paine, S. G., D.Sc., *Imperial College of Science, S.W. 7.*
1920. Palmer, Ray, *Ingleholme, Norton Way, S., Letchworth.*
1914. Pearson, J., D.Sc., *Director, The Museum, Colombo, Ceylon.*
1920. Percival, Prof. J., M.A., F.L.S., *University College, Reading.*
1914. Petherbridge, F. R., M.A., *Sidney Sussex College, Cambridge.*
Orig. Pethybridge, G. H., Ph.D., B.Sc., *Royal College of Science, Dublin, Ireland.*
1914. Pole-Evans, J. B., D.Sc., F.L.S., *Agricultural Department, Pretoria, Transvaal.*
1919. Pomeroy, A. W. J., *Govt. Entomologist, Ibadan, Southern Nigeria.*
1915. Porter, Dr Annie, *Zoological Department, S. African School of Mines and Technology, Johannesburg.*
†1907. Poulton, Prof. E. B., M.A., D.Sc., LL.D., F.R.S., F.L.S., F.G.S., F.Z.S., F.E.S., *Wykeham House, Oxford.*
1920. Prain, Lt.-Col. Sir David, C.M.G., C.I.E., M.A., M.B., F.R.S., LL.D., F.R.S.E., V.M.H., *The Royal Botanic Gardens, Kew.*
1908. Priestley, Prof. J. H., B.Sc., *The University, Leeds.*
Hon. Railliet, Prof., *Alfort, Paris.*
1919. Rayner, Dr. M. C. (Mrs Neilson Jones), *University of London Club,* 21, *Gower Street, W.C.* 1.
1920. Rendle, A. B., M.A., D.Sc., F.R.S., F.L.S., *Keeper of Botany, British Museum (Natural History), Cromwell Road, London, S.W.* 7.
1914. Rennie, J., D.Sc., F.R.S.E., 60, *Desswood Place, Aberdeen.*
1910. Rettie, T., D.Sc., 12, *Ann Street, Edinburgh.*
1914. Roberts, A. W. Rymer, M.A., F.E.S., *School of Zoology, Cambridge.*
1916. Robinson, Wilfred, D.Sc., *Department of Botany, University of Manchester.*
1918. Robson, Robert; *Institute of Agriculture, Chelmsford.*
1920. Roebuck, A., N.D.A., *Harper Adams College, Newport, Salop.*
1907. Rogers, A. G. L., *Ministry of Agriculture and Fisheries,* 6, *St James's Square, London, S.W.* 1.
1920. Russell, E. J., D.Sc., F.C.S., F.R.S., *Rothamsted Experimental Station, Harpenden, Herts.*
1920. Salisbury, E. J., D.Sc., F.L.S., *Botanical Department, University College, London, W.C.* 1.
1914. Salmon, E. S., F.L.S., *S.E. Agricultural College, Wye, Kent.*
1920. Searle, G. O., B.Sc., *School of Botany, Cambridge.*
1920. Seward, Prof. A. C., M.A., D.Sc., F.R.S., F.G.S., *Botany School, Cambridge.*
†Orig. Shipley, Sir A. E., M.A., D.Sc., F.R.S., *Christ's College, Cambridge.*
1920. Small, Prof. J., D.Sc., Ph.C., F.L.S., *Botany School, The University, Belfast, Ireland.*
1920. Smith, A. Malins, M.A., F.L.S., *Biology Department, Technical College, Bradford.*
1920. Smith, E. Holmes, B.Sc., *Botany School, The University, Manchester.*
1920. Smith, W. G., B.Sc., Ph.D., *College of Agriculture, Edinburgh.*
1913. Snell, John, *Bank Chambers, Ormskirk, Lancs.*
Orig. Somerville, Prof. W., M.A., D.Sc., D.Œc., 121, *Banbury Road, Oxford.*
1913. South, F. W., *Agricultural Department, Kuala Lumpur, Federated Malay States.*

1919. Speyer, E. R., *Ridgehurst, Shenley, Herts.*

1920. Spinks, G. T., M.A., *Agricultural and Horticultural Research Station, Long Ashton, Bristol.*

1919. Stone, H., *Forestry School, University of Cambridge.*

1920. Sutherland, Prof. Scott, M.A., *Botany Department, University College, Southampton.*

1920. Sutton, A. W., V.M.H., F.L.S., 9, *Upper Phillimore Gardens, Campden Hill, London, W.* 8.

1920. Sutton, Martin H., F.L.S., *Erlegh Park, Whiteknights, Reading.*

1905. Swanton, E. W., *Brockton, Haslemere, Surrey.*

1920. Tabor, R. J., B.Sc., *Botany School, Imperial College of Science, London.*

1913. Taylor, F. H., *Dalmally Station, via Roma, Queensland.*

1915. Taylor, H. V., *Ministry of Agriculture, London, S.W.* 1.

1914. Theobald, Prof. F. V., *Wye Court, Wye, Kent.*

1920. Thomas, Miss E. N. Miles, D.Sc., F.L.S., *Botanical Department, National Museum of Wales, Cardiff.*

1920. Thornton, H. G., B.A., *Rothamsted Experimental Station, Harpenden, Herts.*

1915. Treherne, R. C., *Agassiz, British Columbia.*

1920. Trow, Principal A. H., D.Sc., F.L.S., *University College, Cardiff.*

1913. Urich, F. W., *Board of Agriculture, Port of Spain, Trinidad.*

1914. Vassall, Archer, M.A., F.Z.S., *Harrow School, Harrow.*

1920. Wager, H. H., D.Sc., F.R.S., F.L.S., "*Hendre,*" *Horsforth Lane, Far Headingly, Leeds.*

1920. Wakefield, Miss E. M., F.L.S., *Royal Botanic Gardens, Kew.*

1905. Walker, A. D., *Ulcombe Place, Nr Maidstone.*

1914. Wallace, Prof. R., *The University, Edinburgh.*

1920. Waller, John Claude, B.A., *S.E. Agricultural College, Wye, Kent.*

Orig. Warburton, Cecil, M.A., *Yew Garth, Grantchester, Cambridge.*

1920. Ware, W. M., B.Sc., *Brookfield, Fremington, Barnstaple, N. Devon.*

1914. Waterston, Capt. J., M.A., B.Sc., *Imperial Bureau of Entomology, Nat. Hist. Museum, South Kensington, S.W.* 7.

1920. Watson, W., A.L.S., *Curator of the Royal Botanic Gardens, Kew, Surrey.*

1920. Weiss, Prof. F. E., D.Sc., F.R.S., F.L.S., *Botany School, The University, Manchester.*

1905. Wellcome, Henry S., *Snow Hill Buildings, London, E.C.* 1.

1918. West, Cyril, D.Sc., A.R.C.S., D.I.C., F.L.S., 7, *Colfe Road, Forest Hill, S.E.* 23.

1905. Wilks, Rev. W., M.A., *Royal Horticultural Society, Vincent Square, Westminster, S.W.*

1912. Williams, C. B., B.A., 20, *Slatey Road, Birkenhead.*

1909. Williamson, H. C., M.A., D.Sc., *Fishery Board of Scotland, Aberdeen.*

1920. Willis, J. C., M.A., D.Sc., F.R.S., *Beechcroft, Clarendon Road, Cambridge.*

1920. Wilson, Malcolm, R.B.S., 31, *Warder Road, Trinity, Edinburgh.*

1914. Wormald, H., D.Sc., A.R.C.S., *S.E. Agricultural College, Wye, Kent.*

1917. Wright, F. S., *Ministry of Agriculture, London, S.W.* 1.

1916. Wright, Herbert, *Mincing Lane House, London, E.C.* 3.

---

† Indicates members who have compounded for their annual subscription.

LAWS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS.

1. The Association shall be named "The Association of Economic Biologists."

2. The objects of the Association shall be to promote the study of Economic Biology.

3. The Association shall consist of Honorary and Ordinary Members.

4. Each candidate for ordinary membership shall be nominated by two members. Such nomination shall be approved by the Council and confirmed by a vote of two-thirds of the members present and voting at the next General Meeting.

Every member elected shall receive notice from the Secretary and shall continue a member until his written resignation shall be received by the Secretary, or until membership be forfeited under the Laws.

Ordinary Members shall pay an annual subscription of One Guinea, due on January 1st of each year, or may compound for their subscription with a sum of fifteen guineas.

All Ordinary Members on first election shall pay an entrance fee of half-a-guinea.

5. Ordinary Members shall be entitled to admission to all the meetings of the Association, to vote thereat, to present papers, to take part in discussions and to receive a copy of the Association's publications.

Each member shall be entitled to introduce personally non-members to the Association's meetings.

6. Honorary Members shall be persons, *not subjects of the British Crown*, who have contributed in an eminent degree to the advancement of the science of Economic Biology. They shall be recommended by a majority of the whole Council and elected in the same manner as Ordinary Members.

The number of Honorary Members shall not at any time exceed *twelve* and not more than *two* shall be elected in any one year.

Honorary Members shall not be liable to any payments and shall each receive a copy of the Association's publications.

Their privileges shall be the same as those of Ordinary Members, but they shall not be entitled to vote at the meetings.

7. The Council shall have power, at any of their meetings, by two-thirds of the votes of those present and voting, to terminate the membership of any member whose subscription shall be one year or more in arrears, or whose membership shall, from any other cause, be undesirable. No member whose subscription is in arrears shall be entitled to vote at a General Meeting or to receive the Association's publications, nor shall any publication be sent to a new member until his entrance fee and subscription shall have been received.

8. All meetings shall be announced by circular addressed to all Members resident in the United Kingdom. The place and time of the meetings shall be decided by the Council; ten shall be a quorum at such a meeting.

9. An Annual General Meeting shall be held and shall ordinarily be the General Meeting falling nearest to the end of the year or as the Council shall decide.

At this meeting the order of business shall be:

1. The reading of the minutes of the previous meeting.
2. The reading of a report of the Council on the work of the past year.
3. The statement of the Treasurer.
4. The election of members.
5. The election of Officers and other Members of the Council.
6. Other business.

10. The business of the Association shall be conducted by a Council consisting of a President, not more than five Honorary Vice-Presidents, a Treasurer, one or more Secretaries, and twelve other members.

11. The Council shall nominate the Officers and other Members of the Council for the ensuing year. A list of such nominations shall be sent to all members resident in the United Kingdom at least three weeks before the Annual General Meeting. The President shall designate two Members of Council to act as Vice-Presidents.

Any Member proposing an addition to, or an alteration in, the list must inform the Honorary Secretary by letter at least ten days before the Annual General Meeting.

The nominations shall be confirmed by the members present at the Annual General Meeting and a ballot shall be taken in the event of any additions or alterations being proposed.

12. The Council may fill up any vacancy that may occur in the list of Officers and Council.

13. The Council shall meet at such times as they may determine; six members shall form a quorum.

The Council shall purchase such books, instruments, specimens, furniture and other necessaries as may be required, pass the accounts and authorise their payment, and generally manage the affairs and administer the funds of the Association.

14. The Council shall appoint from the Members of the Association an Editorial Committee who shall be responsible for the publications.

15. At a Council Meeting, prior to the Annual General Meeting, the Council shall appoint one or more Auditors to audit the Treasurer's Accounts.

16. All properties of the Association, both present and future, shall be deemed to be vested in the Council of the Association for the time being, in conformity with the provisions of the Literary and Scientific Institutions Act, 1854.

17. No new Law shall be made nor any Law altered except on the proposition of the Council or the requisition of at least ten members addressed to the Honorary Secretary. The new Laws or alterations of Laws shall be proposed in writing, signed by the requisitionists and delivered to the Honorary Secretary a month before an Extraordinary General Meeting, which shall be called for the purpose.

Such proposed new Laws or alterations in the Laws shall be printed in the circular convening the Meeting, and sent to all members resident in the United Kingdom at least two weeks before the date of such Meeting.

No new laws, alterations or amendments shall be passed except by a two-thirds majority, when not less than fifteen members are present and voting.

CAMBRIDGE: PRINTED BY
J. B. PEACE, M.A.,
AT THE UNIVERSITY PRESS

Vol. VI, No. 1 September, 1919

THE ANNALS OF APPLIED BIOLOGY

THE OFFICIAL ORGAN OF THE ASSOCIATION
OF ECONOMIC BIOLOGISTS

EDITED BY

E. E. GREEN, Way's End, Camberley (late Government Entomologist, Ceylon)

WITH THE ASSISTANCE OF

Professor B. T. P. BARKER, National Fruit and Cider Institute, Bristol
Dr S. E. CHANDLER, Imperial Institute, London
F. J. CHITTENDEN, Royal Horticultural Society's Gardens, Wisley
J. C. F. FRYER, Board of Agriculture and Fisheries, London
Professor F. W. GAMBLE, The University, Birmingham
Professor PERCY GROOM, Imperial College of Science and Technology, London
Dr A. D. IMMS, Rothamsted Experimental Station, Harpenden
Professor R. NEWSTEAD, The University, Liverpool
Professor J. H. PRIESTLEY, The University, Leeds

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, Manager
LONDON: FETTER LANE, E.C. 4
also
H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
WILLIAM WESLEY & SON, 28, ESSEX STREET, LONDON, W.C. 2
PARIS: LIBRAIRIE HACHETTE & CIE.
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TORONTO: J. M. DENT & SONS, LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

Price Ten Shillings net

The Association of Economic Biologists

President

Professor J. B. FARMER, D.Sc., F.R.S.

Vice-Presidents

Professor CARPENTER, M.R.I.A.
Professor STANLEY GARDINER, F.R.S.
Professor HICKSON, F.R.S.
R. STEWART MacDOUGALL, D.Sc.
A. E. SHIPLEY, D.Sc., F.R.S.

Hon. Treasurer

J. C. F. FRYER, Esq.,
The Pathological Laboratory,
Royal Gardens,
Kew.

Hon. Sec. for Publications

E. E. GREEN, Esq.,
Way's End,
Camberley.

Hon. Secretary

S. A. NEAVE, D.Sc.,
89, Queen's Gate, S.W. 7

Council

Lt.-Col. ALCOCK, I.M.S., F.R.S.
Prof. B. T. P. BARKER
S. E. CHANDLER, D.Sc.
F. J. CHITTENDEN
A. D. COTTON
A. D. IMMS, D.Sc.
R. T. LEIPER, D.Sc.
G. A. K. MARSHALL, D.Sc.
A. G. L. ROGERS
Prof. W. SOMERVILLE

CONTENTS OF Vol. VI, No. 1

PAGE

1. Physiological Pre-determination: the Influence of the Physiological Condition of the Seed upon the Course of Subsequent Growth and upon the Yield: V. Review of Literature. Chapter IV. By F. Kidd, M.A. (Cantab.), D.Sc. (Lond.), and C. West, A.R.C.Sc., D.Sc. (Lond.), F.L.S. (With Plate I and 3 Text-figures) . . . 1
2. Studies in Bacteriosis. III. A Bacterial Leaf-spot disease of *Protea Cynaroides*, exhibiting a host reaction of possibly Bacteriolytic Nature. By S. G. Paine and H. Stansfield. (With Plate II and 4 Text-figures) . . . 27
3. On the occurrence of the Immature Stages of Anopheles in London. By F. E. Jarvis . . . 40
4. The distribution of Parasite-infected Fish. By H. C. Williamson, M.A., D.Sc. (With 4 Text-figures) . . . 48
5. Observations on the habits of certain Flies, especially of those breeding in manure. By J. E. M. Mellor, B.A. (With 6 Text-figures and 4 Charts) . . . 53

Cambridge University Press

Manuring for Higher Crop Production. By E. J. Russell, D.Sc., Director of the Rothamsted Experimental Station Second edition, revised and extended. With 17 illustrations. Demy 8vo. 4s net.

"An authentic and lucid record of modern researches into soils and manuring, with deductions and recommendations which the husbandman will find of great assistance. . . . The war period has given us no more opportune or valuable book for farmers."—*The Times*

A Student's Book on Soils and Manures. By E. J. Russell, D.Sc. With 41 illustrations. Crown 8vo. Second edition, revised and enlarged. 6s 6d net. Cambridge Farm Institute Series.

"The admirable little volume before us is a pleasing example of the success Dr Russell has achieved in proving the compatibility of science and practice in respect to the treatment and use of soils. The reader will find here what is best in theory presented in a form that will make it easy for him to reconcile it with the stern realities of practice."—*The Field*

The Fertility of the Soil. By E. J. Russell, D.Sc. With 9 illustrations. 16mo. Cloth, 2s net; lambskin, 3s net. Cambridge Manuals Series.

British Grasses and their Employment in Agriculture. By S. F. Armstrong, F.L.S., of the School of Agriculture, Cambridge. With 175 illustrations. Demy 8vo. 6s net.

"The Agricultural student, for whom primarily the volume has been written, will find in it a useful guide to his study of the grasses which form our meadows and pastures, and valuable help in their practical employment and treatment."
The Journal of Botany

Inorganic Plant Poisons and Stimulants. By Winifred E. Brenchley, D.Sc., F.L.S. With 19 illustrations. Royal 8vo. 6s net. Cambridge Agricultural Monographs.

"To those who are interested in the subject, we would strongly recommend this work, as one which will serve to enlighten many difficult problems that assail both the scientific and practical man."—*Farm and Home*

Plants Poisonous to Live Stock. By Harold C. Long, B.Sc. (Edin.), of the Board of Agriculture and Fisheries. With frontispiece. Royal 8vo. 6s 6d net. Cambridge Agricultural Monographs.

"Mr Long's intention in this book has been to collect a number of facts . . . which are obviously of the first importance to all breeders of live stock. . . . The volume is an excellent example of the work which Cambridge is doing for agriculture."
The New Statesman

The Production and Utilisation of Pine Timber in Great Britain. Part I. Production. By E. R. Burdon, M.A., Investigator in Timber, and A. P. Long, B.A., Assistant Investigator. Cambridge School of Forestry Bulletins.

No. 1. Sample Plots of Scots Pine at Woburn. Demy 8vo. Paper covers. 1s 6d net.
No. 2. Sample Plot of Scots Pine at King's Lynn. Demy 8vo. Paper covers. 9d net.

Fungoid and Insect Pests of the Farm. By F. R. Petherbridge, M.A., Biological Adviser, School of Agriculture, Cambridge. With 54 illustrations. Large crown 8vo. 5s 6d net. Cambridge Farm Institute Series.

"Will be exceedingly useful. . . . It supplies in a plain, lucid way just what the farmer wants to know concerning the identification and treatment of the more common and destructive of these enemies."—*The Times*

Cambridge University Press
London, Fetter Lane, E.C. 4: C. F. Clay, Manager

THE ANNALS OF APPLIED BIOLOGY

In the *Annals of Applied Biology* papers will be published concerning the economic aspects of agriculture, botany, plant-breeding, plant-pathology, mycology, horticulture, forestry, helminthology, entomology, veterinary zoology, medical zoology, and marine zoology.

Contributors to *The Annals* are asked to send type-written articles if possible, and as far as possible to make illustrations in a form suitable for reproduction as text-figures. Contributors will receive free fifty copies of articles only.

Editorial communications should be addressed to E. E. Green, at Way's End, Camberley, Surrey.

Terms of subscription.

Members of the Association will receive *The Annals* free. To others, the annual subscription price, including postage to any part of the world, for a single copy of each of the four parts making up the annual volume, is 33*s*. 6*d*. net; single copies 10*s*. net each. Subscriptions for *The Annals* are payable in advance and should be sent to Mr C. F. CLAY, Cambridge University Press, Fetter Lane, London, E.C. 4, either direct or through any bookseller.

Volumes I, II, III, IV and V now ready. Price, in four parts, paper covers, 33*s*. 6*d*. net each; bound in Buckram, 44*s*. net each.

Quotations can be given for binding cases and for binding Subscribers' Sets.

The publishers have appointed the University of Chicago Press agents for the sale of *The Annals of Applied Biology* in the United States of America and have authorised them to charge the following prices: annual subscription, post free, $8.00, single copies, $2.50.

Claims for missing numbers should be made within the month following that of regular publication.

CAMBRIDGE: PRINTED BY J. B. PEACE, M.A., AT THE UNIVERSITY PRESS.

Vol. VI, Nos. 2 & 3 December, 1919

THE ANNALS OF APPLIED BIOLOGY

THE OFFICIAL ORGAN OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS

EDITED BY
E. E. GREEN, Way's End, Camberley (late Government Entomologist, Ceylon)
WITH THE ASSISTANCE OF THE COUNCIL

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, Manager
LONDON: FETTER LANE, E.C. 4
also
H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
WILLIAM WESLEY & SON, 28, ESSEX STREET, LONDON, W.C. 2
PARIS: LIBRAIRIE HACHETTE & CIE.
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TORONTO: J. M. DENT & SONS, LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

Price Fifteen Shillings net

The Association of Economic Biologists

President

PROFESSOR J. B. FARMER, D.Sc., F.R.S.

Vice-Presidents

PROFESSOR W. SOMERVILLE
A. G. L. ROGERS, Esq.

Hon. Treasurer

J. C. F. FRYER, Esq.,
The Pathological Laboratory,
Royal Gardens,
Kew.

Hon. Sec. for Publications

E. E. GREEN, Esq.,
Way's End,
Camberley.

Hon. Secretary (General and Zoology)

S. A. NEAVE, D.Sc.,
89, Queen's Gate, S.W. 7

Hon. Secretary (Botany)

W. B. BRIERLEY, Esq.,
Rothamsted Experimental Station

Council

LT.-COL. ALCOCK, I.M.S., F.R.S.
PROF. B. T. P. BARKER
S. E. CHANDLER, D.Sc.
F. J. CHITTENDEN
A. D. COTTON
A. D. IMMS, D.Sc.
R. T. LEIPER, D.Sc.
G. A. K. MARSHALL, D.Sc.
A. G. L. ROGERS
PROF. W. SOMERVILLE

CONTENTS OF VOL. VI, NOS. 2 & 3

PAGE

1. A Phytophthora Rot of Pears and Apples. By H. WORMALD, D.Sc. (Lond.), A.R.C.Sc. (With 2 Text-figures and Plate III) . 89
2. Notes on the Biology of *Necrobia ruficollis*, Fabr. [Coleoptera, Cleridae]. By HUGH SCOTT, M.A., Sc.D. (Cantab.). (With 2 Text-figures) 101
3. On the Life-History of "Wireworms" of the Genus *Agriotes*, Esch., with some Notes on that of *Athous Haemorrhoidalis*, F. Part I. By A. W. RYMER ROBERTS, M.A. (With 5 Text-figures and Plate IV) 116
4. On a Coenurus in the Rat. By M. TURNER, B.Sc. (With 1 Text-figure) 136
5. Some Factors in Plant Competition. By WINIFRED E. BRENCHLEY, D.Sc. (With 10 Text-figures and Plate V) 142
6. A Contribution to the Life-History of the Larch Chermes (*Cnaphalodes strobilobius*, Kalt.). By EDWARD R. SPEYER, F.E.S., M.A. (Oxon.), Carnegie Scholar. (With Diagram and Plates VI and VII) . . 171
7. Studies in Bacteriosis. IV.—"Stripe" Disease of Tomato. By SYDNEY G. PAINE and W. F. BEWLEY. (With 5 Text-figures and Plates VIII and IX) 183
8. Notes on the Life-History of *Ephestia kuhniella*. By RAYMOND V. WADSWORTH 203
9. Notes. By J. C. F. FRYER 207
10. Review 210

Cambridge University Press

Cattle and the Future of Beef-Production in England. By K. J. J. MACKENZIE, M.A. With a Preface and Chapter by F. H. A. MARSHALL, Sc.D. Demy 8vo. 7s 6d net.

"One of the best treatises issued in recent years on the breeding and feeding of cattle. . . . Mr Mackenzie's main plea is for better bred, better handled, and more economically finished animals. . . . The chapters on dual purpose cattle, pedigree breeding, dairy shorthorns, and future possibilities are generally excellent. . . . Dr Marshall's chapter on physiology contains a great deal of valuable matter in small compass."—The Agricultural Correspondent of *The Glasgow Herald*

Plants Poisonous to Live Stock. By HAROLD C. LONG, B.Sc. (Edin.), of the Board of Agriculture and Fisheries. With frontispiece. Royal 8vo. 6s 6d net. Cambridge Agricultural Monographs.

"Mr Long's intention in this book has been to collect a number of facts . . . which are obviously of the first importance to all breeders of live stock. . . . The volume is an excellent example of the work which Cambridge is doing for agriculture."
The New Statesman

Manuring for Higher Crop Production. By E. J. RUSSELL, D.Sc., Director of the Rothamsted Experimental Station Second edition, revised and extended. With 17 illustrations. Demy 8vo. 4s net.

"An authentic and lucid record of modern researches into soils and manuring, with deductions and recommendations which the husbandman will find of great assistance. . . . The war period has given us no more opportune or valuable book for farmers."—*The Times*

A Student's Book on Soils and Manures. By E. J. RUSSELL, D.Sc. With 41 illustrations. Crown 8vo. Second edition, revised and enlarged. 6s 6d net. Cambridge Farm Institute Series.

"The admirable little volume before us is a pleasing example of the success Dr Russell has achieved in proving the compatibility of science and practice in respect to the treatment and use of soils. The reader will find here what is best in theory presented in a form that will make it easy for him to reconcile it with the stern realities of practice."—*The Field*

The Fertility of the Soil. By E. J. RUSSELL, D.Sc. With 9 illustrations. 16mo. Cloth, 2s net; lambskin, 3s net. Cambridge Manuals Series.

British Grasses and their Employment in Agriculture. By S. F. ARMSTRONG, F.L.S., of the School of Agriculture, Cambridge. With 175 illustrations. Demy 8vo. 6s net.

"The Agricultural student, for whom primarily the volume has been written, will find in it a useful guide to his study of the grasses which form our meadows and pastures, and valuable help in their practical employment and treatment."
The Journal of Botany

Inorganic Plant Poisons and Stimulants. By WINIFRED E. BRENCHLEY, D.Sc., F.L.S. With 19 illustrations. Royal 8vo. 6s net. Cambridge Agricultural Monographs.

"To those who are interested in the subject, we would strongly recommend this work, as one which will serve to enlighten many difficult problems that assail both the scientific and practical man."—*Farm and Home*

Fungoid and Insect Pests of the Farm. By F. R. PETHERBRIDGE, M.A., Biological Adviser, School of Agriculture, Cambridge. With 54 illustrations. Large crown 8vo. 5s 6d net. Cambridge Farm Institute Series.

"Will be exceedingly useful. . . . It supplies in a plain, lucid way just what the farmer wants to know concerning the identification and treatment of the more common and destructive of these enemies."—*The Times*

Cambridge University Press
London, Fetter Lane, E.C. 4 : C. F. Clay, Manager

THE ANNALS OF APPLIED BIOLOGY

In the *Annals of Applied Biology* papers will be published concerning the economic aspects of agriculture, botany, plant-breeding, plant-pathology, mycology, horticulture, forestry, helminthology, entomology, veterinary zoology, medical zoology, and marine zoology.

Contributors to *The Annals* are asked to send type-written articles if possible, and as far as possible to make illustrations in a form suitable for reproduction as text-figures. Contributors will receive free fifty copies of articles only.

Editorial communications should be addressed to E. E. Green, at Way's End, Camberley, Surrey.

Terms of subscription.

Members of the Association will receive *The Annals* free. To others, the annual subscription price, including postage to any part of the world, for a single copy of each of the four parts making up the annual volume, is 33*s.* 6*d.* net; single copies 10*s.* net each. Subscriptions for *The Annals* are payable in advance and should be sent to Mr C. F. Clay, Cambridge University Press, Fetter Lane, London, E.C. 4, either direct or through any bookseller.

Volumes I, II, III, IV and V now ready. Price, in four parts, paper covers, 33*s.* 6*d.* net each.

Quotations can be given for binding cases and for binding Subscribers' Sets; also for bound copies of back volumes.

The publishers have appointed the University of Chicago Press agents for the sale of *The Annals of Applied Biology* in the United States of America and have authorised them to charge the following prices: annual subscription, post free, $8.50, single copies, $2.50.

Claims for missing numbers should be made within the month following that of regular publication.

CAMBRIDGE: PRINTED BY J. B. PEACE, M.A., AT THE UNIVERSITY PRESS.

Vol. VI, No. 4 April, 1920

THE ANNALS OF APPLIED BIOLOGY

THE OFFICIAL ORGAN OF THE ASSOCIATION
OF ECONOMIC BIOLOGISTS

EDITED BY
E. E. GREEN, Way's End, Camberley (late Government Entomologist, Ceylon)
WITH THE ASSISTANCE OF THE COUNCIL

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, Manager
LONDON: FETTER LANE, E.C. 4
also
H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
WILLIAM WESLEY & SON, 28, ESSEX STREET, LONDON, W.C. 2
PARIS: LIBRAIRIE HACHETTE & CIE.
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TORONTO: THE MACMILLAN CO. OF CANADA, LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

Price Ten Shillings net

The Association of Economic Biologists

President

PROFESSOR J. B. FARMER, D.SC., F.R.S.

Vice-Presidents

PROFESSOR W. SOMERVILLE
A. G. L. ROGERS, ESQ.

Hon. Treasurer

J. C. F. FRYER, ESQ.,
The Pathological Laboratory,
Royal Gardens,
Kew.

Hon. Sec. for Publications

E. E. GREEN, ESQ.,
Way's End,
Camberley.

Hon. Secretary (General and Zoology)

S. A. NEAVE, D.SC.,
89, Queen's Gate, S.W. 7

Hon. Secretary (Botany)

W. B. BRIERLEY, ESQ.,
Rothamsted Experimental Station

Council

LT.-COL. ALCOCK, I.M.S., F.R.S.
PROF. B. T. P. BARKER
S. E. CHANDLER, D.SC.
F. J. CHITTENDEN
A. D. COTTON
A. D. IMMS, D.SC.
R. T. LEIPER, D.SC.
G. A. K. MARSHALL, D.SC.
A. G. L. ROGERS
PROF. W. SOMERVILLE

CONTENTS OF VOL. VI, No. 4

PAGE

1. On the Relations between Growth and the Environmental Conditions of Temperature and Bright Sunshine. By WINIFRED E. BRENCHLEY, D.Sc. (With 13 Text-figures) 211
2. *Glomerella cingulata* (Stoneman) Spauld. and v. Sch. and its Conidial forms, *Glœosporium piperatum* E. and E. and *Colletotrichum nigrum* E. and Hals., on Chillies and *Carica papaya*. By JEHANGIR FARDUNJI DASTUR, M.Sc. (With Plate X) 245
3. Field Experiments on the Chemotropic Responses of Insects. By A. D. IMMS, M.A., D.Sc., and M. A. HUSAIN, B.A. (With 1 Text-figure) . 269
4. On Forms of the Hop (*Humulus Lupulus* L. and *H. americanus* Nutt.) Resistant to Mildew (*Sphaerotheca Humuli* (DC.) Burr.). By E. S. SALMON 293
5. On the Sexual Forms of *Aphis saliceti*, Kaltenbach. By MAUD D. HAVILAND 311
6. Proceedings of the Association of Economic Biologists 314
7. I. The Administrative Problem. By Sir A. D. HALL, K.C.B., F.R.S. . 317
8. II. The Training Problem. By Professor V. H. BLACKMAN, Sc.D., F.R.S. 322
9. III. The Agricultural Problem. By E. J. RUSSELL, D.Sc., F.R.S. . . 326
10. IV. The Horticultural Problem. By F. J. CHITTENDEN, F.L.S., V.M.H. . 330
11. V. The Forestry Problem. By Professor W. SOMERVILLE, M.A., D.Sc., D.Œc. 333
12. VI. General Discussion 339
13. List of Members of the Association of Economic Biologists for 1920 . . 349
14. Laws of the Association of Economic Biologists 355

Cambridge University Press

Cattle and the Future of Beef-Production in England. By K. J. J. MACKENZIE, M.A. With a Preface and Chapter by F. H. A. MARSHALL, Sc.D. Demy 8vo. 7s 6d net.

"One of the best treatises issued in recent years on the breeding and feeding of cattle.... Mr Mackenzie's main plea is for better bred, better handled, and more economically finished animals.... The chapters on dual purpose cattle, pedigree breeding, dairy shorthorns, and future possibilities are generally excellent.... Dr Marshall's chapter on physiology contains a great deal of valuable matter in small compass."—The Agricultural Correspondent of *The Glasgow Herald*

Physiology of Farm Animals. By T. B. WOOD, C.B.E., F.R.S., and F. H. A. MARSHALL, Sc.D. Part I, General. By F. H. A. Marshall. Demy 8vo. With 105 illustrations. 16s net.

This book is intended primarily for students of agriculture who may wish to obtain some knowledge of the simpler physiological processes as they occur in farm animals. It should also be of use to veterinary students.

Plants Poisonous to Live Stock. By HAROLD C. LONG, B.Sc. (Edin.), of the Board of Agriculture and Fisheries. With frontispiece. Royal 8vo. 6s 6d net. Cambridge Agricultural Monographs.

"Mr Long's intention in this book has been to collect a number of facts... which are obviously of the first importance to all breeders of live stock.... The volume is an excellent example of the work which Cambridge is doing for agriculture."
The New Statesman

A Course of Practical Chemistry for Agricultural Students. Volume I. By L. F. NEWMAN, M.A., and H. A. D. NEVILLE, M.A., B.Sc. Crown 8vo. 10s 6d net.

This volume deals with the chemistry and physics of the soil; Volume II, of which Part I has already been published (5s net), deals with the chemistry of foods. The exercises are designed to illustrate essential points and require the minimum of apparatus.

Manuring for Higher Crop Production. By E. J. RUSSELL, D.Sc., F.R.S., Director of the Rothamsted Experimental Station. Second edition, revised and extended. With 17 illustrations. Demy 8vo. 4s net.

"An authentic and lucid record of modern researches into soils and manuring, with deductions and recommendations which the husbandman will find of great assistance.... The war period has given us no more opportune or valuable book for farmers."—*The Times*

British Grasses and their Employment in Agriculture. By S. F. ARMSTRONG, F.L.S. With 175 illustrations. Demy 8vo. 6s net.

"The Agricultural student, for whom primarily the volume has been written, will find in it a useful guide to his study of the grasses which form our meadows and pastures, and valuable help in their practical employment and treatment."
The Journal of Botany

Inorganic Plant Poisons and Stimulants. By WINIFRED E. BRENCHLEY, D.Sc., F.L.S. With 19 illustrations. Royal 8vo. 6s net. Cambridge Agricultural Monographs.

"To those who are interested in the subject, we would strongly recommend this work, as one which will serve to enlighten many difficult problems that assail both the scientific and practical man."—*Farm and Home*

Fungoid and Insect Pests of the Farm. By F. R. PETHERBRIDGE, M.A. With 54 illustrations. Large crown 8vo. 5s 6d net. Cambridge Farm Institute Series.

"Will be exceedingly useful.... It supplies in a plain, lucid way just what the farmer wants to know concerning the identification and treatment of the more common and destructive of these enemies."—*The Times*

Cambridge University Press
London, Fetter Lane, E.C. 4: C. F. Clay, Manager

THE ANNALS OF APPLIED BIOLOGY

In the *Annals of Applied Biology* papers will be published concerning the economic aspects of agriculture, botany, plant-breeding, plant-pathology, mycology, horticulture, forestry, helminthology, entomology, veterinary zoology, medical zoology, and marine zoology.

Contributors to *The Annals* are asked to send type-written articles if possible, and as far as possible to make illustrations in a form suitable for reproduction as text-figures. Contributors will receive free fifty copies of articles only.

Editorial communications should be addressed to E. E. Green, at Way's End, Camberley, Surrey.

Terms of subscription.

Members of the Association will receive *The Annals* free. To others, the annual subscription price, including postage to any part of the world, for a single copy of each of the four parts making up the annual volume, is 33*s*. 6*d*. net; single copies 10*s*. net each. Subscriptions for *The Annals* are payable in advance and should be sent to Mr C. F. Clay, Cambridge University Press, Fetter Lane, London, E.C. 4, either direct or through any bookseller.

Volumes I, II, III, IV and V now ready. Price, in four parts, paper covers, 33*s*. 6*d*. net each.

Quotations can be given for binding cases and for binding Subscribers' Sets; also for bound copies of back volumes.

The publishers have appointed the University of Chicago Press agents for the sale of *The Annals of Applied Biology* in the United States of America and have authorised them to charge the following prices: annual subscription, post free, $8.50, single copies, $2.50.

Claims for missing numbers should be made within the month following that of regular publication.

CAMBRIDGE: PRINTED BY J. B. PEACE, M.A., AT THE UNIVERSITY PRESS.

MBL/WHOI LIBRARY
WH 17KS J